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The *Journal* is devoted to original research papers and notes concerning aquatic organisms or environments relevant to Canada. Review articles that are critical appraisals of broad areas of research are also welcomed. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted. Details on submissions are given in guides to authors and typists at the back of each issue.

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Le *Journal* est consacré aux études sur des recherches originales et aux notes concernant les organismes et les environnements aquatiques pertinents au Canada. Des critiques concernant des ouvrages généraux sont aussi appréciés. Des soumissions en anglais ou en francais sont acceptées sans limitations d'origine, sauf si elles ont déjà été publiées ou déposées. Des détails sont fournis dans les guides à la fin de chaque numéro.

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Volume 28, No. 10, October 1971

Journal of the Fisheries Research Board of Canada

This issue

is

Dedicated

to

Edith & Cyril

Berkeley

Edith and Cyril Berkeley — An Appreciation

Can two walk together, except they be agreed? — Amos III, 3

Edith Dunington and Cyril Berkeley met at University College in London in 1898, which by coincidence was the year the Government of Canada established the Fisheries "Board of Management," which evolved into the Fisheries Research Board of Canada. The story goes that Edith was literally thrown into Cyril's arms by a swinging door at University College, and it is equally true that the Board has welcomed them both with open arms since 1919.

The late Mrs Edith Berkeley

For 44 years the Berkeleys were both associated with the Board's station at Nanaimo and they became world leaders in polychaete studies, adding prestige to the Board's research. Mrs Berkeley died in 1963, and Dr Berkeley, who is now 92, is the only living link with the early history of the Nanaimo Station. He continues to carry on their research, and is particularly pleased that this dedicatory issue involves Mrs

Berkeley, commenting "I am, after all, doing no more than carrying on what she taught me."

This issue of the *Journal of the Fisheries Research Board of Canada* is dedicated to Dr Berkeley and to the memory of Mrs Berkeley, and gives expression to the hope that he will be with us for years to come.

Let me tell you something of the interesting background of this couple whose lives spanned almost a century, who travelled most of the world, and who settled half a century ago in a rather obscure town on the east coast of Vancouver Island to make international reputations in invertebrate science.

Dr Cyril J. Berkeley

Edith Dunington was born September 1, 1875, at Tulbagh, South Africa. Her parents, Martha Treglohan and Alfred Dunington, moved to various parts of the world, as her father was an outstanding bridge-building engineer. Edith attended Wimbledon High School and matriculated to the University of London in January 1895. She intended to take up medicine and completed the preliminary scientific examination for the bachelor of medicine degree in 1897. She then continued in pure science in chemistry and zoology. She worked mainly in the zoology department under Professor Weldon, where she first became interested in polychaetes; but she also worked under Dr M. T. Travers in Professor William Ramsay's laboratory, where her future husband was working.

Cyril J. Berkeley, born Cyril J. Bergtheil on December 2, 1878, in London, England, was born within the sound of the bells of Bow Church and is therefore by definition a cockney. His mother, Alice Collins, and father, Louis Bergtheil, were divorced while he was still quite young. The Bergtheil family changed its name, as did many others of German descent, during the early days of the first world war (probably in 1916) to Berkeley.

His mother remarried in 1888, and it was her second husband, Mr Puttick, who first interested Cyril in science. He was not a scientist himself, but he kept many scientific journals in the house and started Cyril's lifelong habit of reading *Nature* regularly. He also took him to lectures at the Royal Institution. Cyril attended the preparatory school for St. Paul's school in 1888 and the newly established science side of St. Paul's school from 1891 to 1895. During 1895–97 he lived with relatives in Nuremberg to learn German and study chemistry at the Industrieschule.

Cyril studied at University College, London, in Professor William Ramsay's chemical research laboratory from 1897 to 1899, during the exciting period in Ramsay's laboratory in which the rare gases were discovered. From 1899 to 1901, he devoted his time to agricultural chemistry and bacteriology at the Agricultural College at Wye.

As mentioned earlier, the Berkeleys met at University College in 1898, and four years later Cyril was appointed bacteriologist in the Agriculture Department of India. He was employed by the Government of Bengal as assistant to Mr Christopher Rawson to study the cultivation and manufacture of indigo under a grant from the Government of India to the Bihar Planter's Association. The natural indigo industry was at this time still attempting to resist the competition of the synthetic dye being produced in Germany, which ultimately took over the market.

The Berkeleys were married February 26, 1902, and sailed the next day for Bombay. They aroused some ship-board interest by fishing with an improvised net for jellyfish as the ship passed through the Suez Canal. Cyril worked most of the next 11 years at Sirsiah near Mozufferpore, Bihar, Bengal. Alfreda Alice Berkeley was born March 3, 1903, and at about age two she was sent back to England to live with her maternal grandmother because of precarious health conditions in India.

While in India Cyril followed portions of the Hooker Trail in the Himalayas with Mr I. H. Burkill (later director of the gardens at Candy in Ceylon), who was collecting aconites for the Imperial Institute. Cyril became interested in the vertical distribution of earthworms during this excursion and collected specimens every 1000 feet up the mountains. They were sent to the Calcutta Museum, which in turn sent them to Dr Michaelsen, then the world authority on oligochaetes, for classification. Some of them proved to be new species, most of them to be new locality records. One, from Sandakphu, Sikkim, was described as *Megascolides bergtheili* in Cyril's honour. G. E. Gates (Indian earthworms. II. *Sclioscolides*, gen.nov. Indian Mus. Rec. 39: 305–310, 1937) later made *bergtheili* the type species of *Sclioscolides*. Edith also climbed in the Himalayas, but did not accompany her husband on this trip.

In 1913 they crossed Canada, visiting Vancouver and the Okanagan on the way back to England. Their daughter Alfreda rejoined them and they returned to the Okanagan in British Columbia in early 1914. They farmed at Lavington, near Vernon, on what had been part of Lord Aberdeen's Coldstream Ranch "raising pigs and producing clotted cream." Cyril even took part in theatricals in the Okanagan.

In 1916–17 Cyril taught bacteriology and Edith zoology in the early days of the University of British Columbia (UBC). They first visited the Nanaimo station in the summer of 1917.

During 1917–19 Cyril worked with the Hercules Powder Company, San Diego, California, on the fermentation of kelp for the production of acetone. Edith continued to work at UBC and again visited the Nanaimo station in the summer of 1918 to collect class material. Both Edith and her daughter Alfreda nursed at the King Edward High School in the Kitsilano area of Vancouver during the 1917 influenza epidemic.

In 1919 the Berkeleys moved permanently to Nanaimo, and for a year and a half Cyril was Assistant Curator of the Biological Station, taking charge during the absences of the Curator, Dr C. McLean Fraser. Edith began her polychaete studies in 1919 as volunteer investigator and continued this research for about 44 years. Shortly after Dr Fraser went to UBC, Cyril became a volunteer investigator at Nanaimo and during the 1920's his research was mainly in the chemical field. However, his scientific interests were very broad, even involving an article in *Nature* in 1943 on "Science, Christianity and Truth."

During the 1920's Edith published several papers on the little-known polychaetous annelids in waters off Nanaimo, B.C., and by about 1930 she persuaded Cyril to join her in the study of polychaete taxonomy. They studied polychaetes from many parts of the world, and they published promptly. Over a period of 64 years they published 92 papers (listed in this issue of the *Journal*), 34 of which were published jointly. And Dr Berkeley is still carrying on their research.

When the Berkeleys decided to live in Nanaimo they bought the house built by the Rev G. W. Taylor, the first Curator of the Biological Station. The property was extensive and overlooked Departure Bay, where the Station was and is situated. They brought with them a piano from India, and it is said that Cyril was an enthusiastic singer of Irish songs and songs based on poems by Rudyard Kipling.

They developed a marvelous garden over the years and their special interest was rhododendrons, plants whose northern limit in Canada is British Columbia. The garden at present contains approximately 100 species of rhododendrons, some now very large. A rhododendron hybrid "Edith Berkeley" was registered by E. and M. Greig in the International Rhododendron Register published by the Royal Horticultural Society, London, in 1958, and application has been made for inclusion in the Register of the "Cyril Berkeley" variety. They also had a fairly complete collection of iris species and Cyril developed several hybrids. And they were generous with their plants and shrubs; no visitor left without receiving something traceable to the Berkeley garden.

Their daughter Alfreda (Mrs A. W. H. Needler) died in 1951. She carried out excellent research on sex reversal in shrimps and oysters, *Gonyaulax*, and related subjects. Two of Alfreda's children are actively engaged in research.

Cyril was elected a fellow of the Canadian Institute of Chemistry in 1919 and was made a life member in 1929. He was elected an Honorary Fellow of the same organization, now the Chemical Institute of Canada, in 1962. He received an LLD from the University of Victoria at the spring convocation in 1968.

Edith died February 25, 1963, and the annual "Edith Berkeley Memorial Lecture" was inaugurated by the University of British Columbia in 1969.

In addition to the rhododendron hybrids named after the Berkeleys and the earthworm mentioned earlier, two polychaetes (*Lepidasthenia berkeleyae* and *Spiophanes*

berkeleyorum) named by M. Pettibone, another polychaete (*Spirorbis berkeleyana* by E. Rioja, and an enteropneust (*Glossobalanus berkeleyi*) by A. Willey, have been named in honour of the Berkeleys. This issue contains articles on many more organisms named in their honour.

The response to this dedicatory issue was so great that unfortunately we had to restrict the number of submissions. All manuscripts submitted on polychaetes were accepted, and several specialists in this field expressed regret that the timing happened to be such that they were unable to contribute.

As great as the Berkeleys' contribution has been to polychaete research, their greatest impact may have been as humanists. They had a great deal of infective charm. They were never too busy to talk to young scientists and their wives. There are scores of people with fond memories of talking with them in their somewhat cluttered laboratory, their quaint home, and their beautiful gardens. It is tempting to relate some of these recollections to show how easy it was for the Berkeleys to bridge the gaps between several generations. But what memories would it be fair to choose?

Edith and Cyril Berkeley "walked together" for 65 years. The Fisheries Research Board of Canada is privileged to honour them with this dedicatory issue of its *Journal*.

J. CAMERON STEVENSON

Publications by Edith and/or Cyril Berkeley

MARY NEEDLER ARAI[1]

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ARAI, M. N. 1971. Publications by Edith and/or Cyril Berkeley. J. Fish. Res. Bd. Canada 28: 1365–1372.

The publications of Edith and Cyril Berkeley are listed, those on their research on Polychaeta being of special interest.

ARAI, M. N. 1971. Publications by Edith and/or Cyril Berkeley. J. Fish. Res. Bd. Canada 28: 1365–1372.

On donne la liste des publications d'Edith et Cyril Berkeley. Leurs travaux de recherches sur les polychètes présentent un intérêt particulier.

Received June 8, 1971

THIS list of publications of my grandparents speaks for itself both as to their contribution to polychaete taxonomy and the wide range of their other interests. It should be noted that prior to the first world war my grandfather published as C. Bergtheil.

I have included one paper that they did not write themselves. In 1964, the type specimens of the Berkeley polychaete collection were transferred to the Smithsonian Institution with the help of Dr Marian H. Pettibone. Pettibone (1967) describes these specimens, and syntypes and paratypes earlier deposited in the British Museum.

I am grateful to Dr W. S. Hoar for checking two papers in the University of British Columbia library.

The fermentation of the indigo-plant.
Transactions of the Chemical Society 85: 870–892, 1904.
C. Bergtheil

The study of fermentation as applied to agriculture.
Agricultural Journal of India 1(1): 68–75, 1906.
C. Bergtheil

The study of fermentation as applied to agriculture. Part II.
Agricultural Journal of India 1(3): 230–236, 1906.
C. Bergtheil

The efficiency of the present process of natural indigo manufacture.
Nature 75: 30, 1906.
C. Bergtheil

The determination of indigotin in commercial indigo and in indigo-yielding plants.
Journal of the Society of Chemical Industry 25: 729–754, 1906.
C. Bergtheil and R. V. Briggs

The determination of indigotin in commercial indigo.
Journal of the Society of Chemical Industry 26: 182–188, 1907.
C. Bergtheil and R. V. Briggs

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This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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The determination of indigotin in indigo-yielding plants.
Journal of the Society of Chemical Industry 26: 1172–1180, 1907.
C. Bergtheil and R. V. Briggs

On the cause of 'Hardness' in the seeds of *Indigofera arrecta*.
Annals of Botany 21(81): 57–60, 1907.
C. Bergtheil and D. L. Day

Research work on natural indigo.
Nature 78: 541, 1908.
C. Bergtheil

A method for producing immediate germination of 'Hard-coated' seeds.
Journal of the Asiatic Society Bengal 3(10): 625, 1908.
R. S. Finlow and C. J. Bergtheil

Indigo reports.
Bihar Planter's Association, Calcutta, India, 1909.
C. Rawson and C. Bergtheil

A study of marine bacteria, Straits of Georgia, B.C.
Transactions of the Royal Society of Canada Series 3, 13(5): 15–43, 1920.
C. Berkeley

Pentose contents of some tissues of marine animals.
Journal of Biological Chemistry 41: liv–lv, 1920.
C. Berkeley

Pentosan- and methylpentosan-splitting enzymes of *Macrocystis pyrifera*.
Journal of Biological Chemistry 41: lvi–lvii, 1920.
C. Berkeley

Pentose mononucleotides of the pancreas of the dogfish (*Squalus sucklii*).
Journal of Biological Chemistry 45: 263–275, 1921.
C. Berkeley

Anaerobic respiration in some pelecypod molluscs. The relation of anaerobic respiration to glycogen.
Journal of Biological Chemistry 46: 579–598, 1921.
C. Berkeley

On pentose compounds in tissues of marine animals.
Transactions of the Royal Society of Canada Series 3, 15(5): 41–47, 1921.
C. Berkeley

On the occurrence of manganese in the tube and tissues of *Mesochaetopterus taylori* Potts, and in the tube of *Chaetopterus variopedatus* Renier.
Biochemical Journal 16(1): 70–77, 1922.
C. Berkeley

An organic constituent of the tube of *Mesochaetopterus taylori* Potts.
Journal of Biological Chemistry 50(1): 113–120, 1922.
C. Berkeley

The oxygen content of waters in the Strait of Georgia.
Contributions to Canadian Biology 1: 71–72, 1922.
C. Berkeley

Polychaetous annelids from the Nanaimo district. Part 1. Syllidae to Sigalionidae.
Contributions to Canadian Biology 1: 203–218, 1923.
E. Berkeley

On the crystalline style as a possible factor in the anaerobic respiration of certain marine mollusks.
Journal of Experimental Zoology 37(5): 477–488, 1923.
C. Berkeley

Is the pentose of the nucleotides formed under the action of insulin?
Nature 112(2820): 724–725, 1923.
C. Berkeley

The distribution of pentose compounds in the pancreatic tissues of the ling cod (*Ophiodon elongatus* Girard).
Journal of Biological Chemistry 58(2): 611–616, 1923.
C. Berkeley

Polychaetous annelids from the Nanaimo district. Part 2. Phyllodocidae to Nereidae.
Contributions to Canadian Biology 2: 285–293, 1924.
E. Berkeley

On a new case of commensalism between echinoderm and annelid.
Canadian Field Naturalist 38: 193, 1924.
E. Berkeley

A note on the organic constitution of Pacific coast kelps.
Contributions to Canadian Biology 2: 503–506, 1925.
C. Berkeley

The crystalline style and anaerobic respiration.
Nature 117(2945): 518, 1926.
C. Berkeley

Some zoological "finds" at Garibaldi.
The B.C. Mountaineer, Special Issue Reporting Scientific Work at the 1926 Summer Camp in Garibaldi Park, B.C., Vancouver, B.C. p. 3–4, 1926.
C. Berkeley

'Hard Seeds' in Leguminosae.
Nature 119(2988): 198, 1927.
C. Berkeley

Polychaetous annelids from the Nanaimo district. Part 3. Leodicidae to Spionidae.
Contributions to Canadian Biology 3: 405–422, 1927.
E. Berkeley

A new genus of Chaetopteridae from the N.E. Pacific: With some remarks on allied genera.
Proceedings of the Zoological Society Part 2: 441–445, 1927.
E. Berkeley

Polychaetous annelids from the Nanaimo district. Part 4. Chaetopteridae to Maldanidae.
Contributions to Canadian Biology 4: 305–316, 1929.
E. Berkeley

The green bodies of the intestinal wall of certain Chaetopteridae.
Quarterly Journal of Microscopical Science 73(3): 465–476, 1930.
C. Berkeley

Symbiosis of *Beroe* and a flagellate.
Contributions to Canadian Biology 6: 13–21, 1930.
C. Berkeley

Polychaetous annelids from the Nanaimo district. Part 5. Ammocharidae to Myzostomidae, with an appendix on some pelagic forms from the Strait of Georgia and the west coast of Vancouver Island.
Contributions to Canadian Biology 6: 65–77, 1930.
E. Berkeley

On a collection of littoral Polychaeta from the west coast of Vancouver Island.
Contributions to Canadian Biology 7: 309–318, 1932.
E. Berkeley and C. Berkeley

Some Capitellidae (Polychaeta) from the N.E. Pacific: With a description of a new genus.
Proceedings of the Zoological Society p. 669–675, 1932.
E. Berkeley and C. Berkeley

Oxidase of the crystalline style.
Nature 131(3299): 94, 1933.
C. Berkeley

The oxidase and dehydrogenase systems of the crystalline style.
Biochemical Journal 27: 1357–1365, 1933.
C. Berkeley

The chemical composition of the crystalline style and of the gastric shield; with some new observations on the occurrence of the style oxidase.
Biological Bulletin 68(1): 107–114, 1935.
C. Berkeley

Some notes on the polychaetous annelids of Elkhorn slough, Monterey Bay, California.
American Midland Naturalist 16: 766–775, 1935.
E. Berkeley and C. Berkeley

Swarming of *Odontosyllis phosphorea* Moore, and of other Polychaeta near Nanaimo, B.C.
Nature 136(3452): 1029, 1935.
E. Berkeley

Plankton of the Bermuda oceanographic expeditions, 3: Notes on Polychaeta.
Zoologica 21: 85–87, 1936.
E. Berkeley

Notes on Polychaeta from the coast of western Canada. Part 1. Spionidae.
Annals and Magazine of Natural History Series 10, 18: 468–477, 1936.
E. Berkeley and C. Berkeley

Occurrence of *Saccocirrus* in western Canada.
Nature 137(3478): 1075, 1936.
E. Berkeley

Notes on Polychaeta from the coast of western Canada. Part 2. Syllidae.
Annals and Magazine of Natural History Series 11, 1: 33–49, 1938.
E. Berkeley and C. Berkeley

Rhamphobrachium longisetosum, n.sp. with some observations on the regeneration of the specialized anterior setae.
Annals and Magazine of Natural History Series 11, 1: 428–435, 1938.
E. Berkeley and C. Berkeley

On a collection of Polychaeta, chiefly from the west coast of Mexico.
Annals and Magazine of Natural History Series 11, 3: 321–346, 1939.
E. Berkeley and C. Berkeley

On a collection of Polychaeta from Southern California.
Bulletin of the Southern California Academy of Sciences 40: 16–60, 1941.
E. Berkeley and C. Berkeley

North Pacific Polychaeta, chiefly from the west coast of Vancouver Island, Alaska, and Bering Sea.
Canadian Journal of Research Section D 20: 183–208, 1942.
E. Berkeley and C. Berkeley

Occurrence of *Ctenodrilus* in the Pacific.
Nature 149(3774): 248, 1942.
C. Berkeley

Biological and oceanographical conditions in Hudson Bay. II. Polychaeta from Hudson Bay.
Journal of the Fisheries Research Board of Canada 6: 129–132, 1943.
E. Berkeley and C. Berkeley

Science, christianity and truth.
Nature 152(3860): 479, 1943.
C. Berkeley

Polychaeta from the western Canadian Arctic region.
Canadian Journal of Research Section D 22: 1–5, 1944.
E. Berkeley and C. Berkeley

Notes on Polychaeta from the coast of western Canada. Part 3. Further notes on Syllidae and some observations on other Polychaeta. Errantia.
Annals and Magazine of Natural History Series 11, 12: 316–335, 1945.
E. Berkeley and C. Berkeley

Polychaeta Errantia.
Fisheries Research Board of Canada Canadian Pacific Fauna 9b(1): 1–100, 1948.
E. Berkeley and C. Berkeley

Morphological characters of *Myriochele heeri* Malmgren.
Nature 164(4162): 239, 1949.
E. Berkeley

Notes on Polychaeta from the coast of western Canada. Part. 4. Polychaeta Sedentaria.
Annals and Magazine of Natural History Series 12, 3: 50–69, 1950.
E. Berkeley and C. Berkeley

A second record of the polychaetous annelid *Potamethus elongatus* (Treadwell).
Journal of the Washington Academy of Sciences 41(10): 332–334, 1951.
E. Berkeley and C. Berkeley

Polychaeta Sedentaria.
Fisheries Research Board of Canada Canadian Pacific Fauna 9b(2): 1–139, 1952.
E. Berkeley and C. Berkeley

Re-discovery of the polychaete worm *Trypanosyllis ingens* Johnson.
Journal of the Fisheries Research Board of Canada 8: 488–490, 1952.
E. Berkeley and C. Berkeley

Swarming of *Nereis succinea* (Leuckart) off the east coast of Canada.
Nature 171(4358): 847, 1953.
E. Berkeley and C. Berkeley

Micronereis nanaimoensis sp.n. with some notes on its life-history.
Journal of the Fisheries Research Board of Canada 10(2): 85–95, 1953.
E. Berkeley and C. Berkeley

Ceanothus velutinus.
Journal of the Royal Horticultural Society 79: 44, 1954.
C. Berkeley

Notes on the life-history of the polychaete *Dodecaceria fewkesi* (nom. n.).
Journal of the Fisheries Research Board of Canada 11: 326–334, 1954.
E. Berkeley and C. Berkeley

Additions to the polychaete fauna of Canada, with comments on some older records.
Journal of the Fisheries Research Board of Canada 11(4): 454–471, 1954.
E. Berkeley and C. Berkeley

A new species and two new records of Polychaeta from eastern Canada.
Canadian Journal of Zoology 34(4): 267–271, 1956.
E. Berkeley and C. Berkeley

On a collection of polychaetous annelids from the northern Banks Island, from the south Beaufort Sea, and from northwest Alaska; together with some new records from the east coast of Canada.
Journal of the Fisheries Research Board of Canada 13: 233–246, 1956.
E. Berkeley and C. Berkeley

Notes on Polychaeta from the east coast of Vancouver Island and from adjacent waters with a description of a new species of *Aricidae*.
Journal of the Fisheries Research Board of Canada 13(4): 541–546, 1956.
E. Berkeley and C. Berkeley

Epidiopatra hupferiana Augener from the north-east Pacific.
Nature 178(4536): 748, 1956.
C. Berkeley

On some pelagic Polychaeta from the northeast Pacific north of latitude 40°N and east of longitude 175°W.
Canadian Journal of Zoology 35: 573–578, 1957.
E. Berkeley and C. Berkeley

Some notes on a collection of Polychaeta from the northeast Pacific south of latitude 32°N.
Canadian Journal of Zoology 36(3): 399–407, 1958.
E. Berkeley and C. Berkeley

Polychaeta of the western Canadian Arctic.
Journal of the Fisheries Research Board of Canada 15: 801–804, 1958.
E. Berkeley and C. Berkeley

Some observations on *Cristispira* in the crystalline style of *Saxidomus giganteus* Deshayes and in that of some other Lamellibranchiata.
Canadian Journal of Zoology 37(1): 53–58, 1959.
C. Berkeley

Notes on some Polychaeta from the west coast of Mexico, Panama, and California.
Canadian Journal of Zoology 38: 357–362, 1960.
E. Berkeley and C. Berkeley

Some further records of pelagic Polychaeta from the northeast Pacific north of latitude 40°N and east of longitude 175°W, together with records of Siphonophora, Mollusca, and Tunicata from the same region.
Canadian Journal of Zoology 38: 787–799, 1960.
E. Berkeley and C. Berkeley

Notes on Polychaeta from California to Peru.
Canadian Journal of Zoology 39(5): 655–664, 1961.
E. Berkeley and C. Berkeley

Swarming of the polychaete *Odontosyllis phosphorea* Moore, var. *nanaimoensis* Berkeley, near Nanaimo, B.C.
Nature 191(4795): 1321, 1961.
E. Berkeley

Indigotin content of woad.
Nature 191(4796): 1414–1415, 1961.
C. Berkeley

Polychaeta from British Columbia; with a note on some western Canadian Arctic forms.
Canadian Journal of Zoology 40(4): 571–577, 1962.
E. Berkeley and C. Berkeley

Toxicity of plankton to *Cristispira* inhabiting the crystalline style of a mollusk.
Science 135(3504): 664–665, 1962.
C. Berkeley

Recollections of Sir William Ramsay and of his work. Part I.
Chemistry in Canada 14: 31–34, 1962.
C. Berkeley

Recollections of Sir William Ramsay and of his work.
Chemistry in Canada 14: 16–19, 1962.
C. Berkeley

The proboscis of *Lycastopsis catarractarum* Feuerborn.
Canadian Journal of Zoology 41: 907–908, 1963.
E. Berkeley and C. Berkeley

Neoteny in larvae of two species of Spionidae.
Canadian Journal of Zoology 41: 149–151, 1963.
E. Berkeley and C. Berkeley

Notes on some pelagic and some swarming Polychaeta taken off the coast of Peru.
Canadian Journal of Zoology 42: 121–134, 1964.
E. Berkeley and C. Berkeley

Records of some species of Polychaeta new to British Columbia and of extensions in distribution of some others.
Canadian Journal of Zoology 44: 839–849, 1966.
C. Berkeley

Type-specimens of polychaetes described by Edith and Cyril Berkeley (1923–1964).
Proceedings of the United States National Museum 119(3553): 1–23, 1967.
M. H. Pettibone

A checklist of Polychaeta recorded from British Columbia since 1923, with references to name changes, descriptions and synonymies. I. Errantia.
Canadian Journal of Zoology 45: 1049–1059, 1967.
C. Berkeley

A checklist of Polychaeta recorded from British Columbia since 1923, with references to name changes, descriptions, and synonymies. II. Sedentaria.
Canadian Journal of Zoology 46: 557–567, 1968.
C. Berkeley

Records of earthworms from Vancouver, British Columbia.
Journal of the Fisheries Research Board of Canada 25(1): 205, 1968.
C. Berkeley

Revision of *Metavermilia* Bush (Polychaeta, Serpulidae), with Descriptions of Three New Species from off Portugal, Gulf of Guinea, and Western Indian Ocean

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The serpulid genus *Metavermilia* Bush 1904, is emended and revalidated for four species: *M. multicristata* (Philippi), the type-species and formerly placed in *Vermiliopsis*, from the Mediterranean Sea and northeast Atlantic, *M. annobonensis* n.sp. from the Gulf of Guinea, *M. taenia* n.sp. from the Bay of Portugal, and *M. nates* n.sp. from the western Indian Ocean. The relationship of *Metavermilia* to the closely related genera *Vermiliopsis* Saint-Joseph and *Pseudovermilia* Bush is discussed. An apparently new form of parasitism (organisms of uncertain systematic position) in serpulid polychaetes was observed on the gill filaments of *M. nates*.

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L'auteur revise et revalide le genre de serpulides *Metavermilia* Bush 1904, à la suite de l'étude de quatre espèces: *M. multicristata* (Philippi), l'espèce-type auparavant assignée à *Vermiliopsis* et provenant de la Méditerranée et de l'Atlantique Nord-Oriental; *M. annobonensis* nov.sp. du Golfe de Guinée; *M. taenia* nov.sp. de la baie du Portugal et *M. nates* nov.sp. de l'océan Indien occidental. Il décrit les relations qui existent entre *Metavermilia* et les genres voisins *Vermiliopsis* Saint-Joseph et *Pseudovermilia* Bush. Il a observé sur les filaments branchiaux de *M. nates* une forme de parasitisme (organismes de position systématique douteuse) apparemment nouvelle chez les polychètes serpulides.

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MARENZELLER (1893 p. 40) observed that some of the serpulid species referred to the genus *Vermilia* Lamarck had similar thoracic setae, including simple, tapered, more-or-less limbate, capillary, and sickle setae. For the species with thoracic sickle setae, Saint-Joseph (1894 p. 262) proposed the genus *Vermiliopsis*. Bush (1904, 1907a, b, 1910) proposed a more sophisticated classification of the species previously referred to *Vermilia* and *Vermiliopsis*, together with some species considered to be new. Chiefly based on the development of the thoracic membranes, the general form of the abdominal setae and uncini, and the terminal tooth of the uncini she distinguished four genera: *Vermiliopsis*, *Paravermilia*, *Metavermilia*, and *Pseudovermilia*, the last three being new. Bush's classification was a tentative one and was based largely on literature. It was followed only by Moore (1923), who described a new species under the generic name *Metavermilia* (*M. multiannulata*), a species referred herein to *Vermiliopsis* sensu stricto. In her catalogue, Hartman (1959) included Bush's three genera under *Vermiliopsis* and placed in synonymy some of Bush's species.

In some previous papers (*Zibrowius* 1968a, b, 1969b, 1970), when describing several new species referable to *Vermiliopsis* sensu lato (sensu Saint-Joseph, Fauvel, Hartman), it was shown that several groups of closely related species could be distinguished. As a first step towards a revision of the heterogeneous group of species referred to *Vermiliopsis*, it was suggested (*Zibrowius* 1970 p. 123–124) that *Vermiliopsis* sensu stricto include *V. infundibulum* (Philippi 1844) (revised diagnosis in Zibrowius

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1968b p. 1206 footnote), *V. richardi* Fauvel 1909, and *V. monodiscus* Zibrowius 1968b, and to revalidate the genus *Pseudovermilia* Bush 1904, for species chiefly characterized by uncini with the anterior tooth bifurcate. It was emphasized, too, that in the present state of our knowledge, it was not possible to find a satisfactory reclassification of the remaining species differing from *Vermiliopsis* sensu stricto and *Pseudovermilia*.

In this regard it should be noted that the deep-water species from off California described as *Vermiliopsis biformis* by Hartman (1960 p. 164 pl. 18–19; 1969 p. 111–112) is referable to the genus *Hyalopomatus* Marenzeller, as revised by Zibrowius (1969a): only six thoracic setigerous segments, five of them uncinigerous; first thoracic segment ("collar segment") with special setae (not simple limbate setae, as in the posterior segments); absence of thoracic sickle setae ("*Apomatus* setae"); form of the uncini.

The discovery of three new species showing affinities to *Vermiliopsis multicristata* (Philippi), the type species of *Metavermilia* Bush 1904, has prompted me to revalidate this genus for the four species.

The serpulids covered in this report are deposited in the British Museum (Natural History), London (BMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Musée Océanographique de Monaco (MOM), Universitetets Zoologiske Museum, Copenhagen (UZM), and in the author's personal collection. The types of the new species are deposited in the United States National Museum, Washington (USNM).

Vermiliopsis Saint-Joseph 1894, sensu stricto; emended Zibrowius 1970

Type-species — *Vermilia multivaricosa* Mörch 1863, designated by Bush (1904 p. 223). Mediterranean. = *Vermiliopsis infundibulum* (Philippi 1844). (Not *Serpula infundibulum* Linnaeus 1788. Indian Ocean. Indeterminable.) Gender: female.

According to Zibrowius (1968b, 1970), the following species are referred to *Vermiliopsis* sensu stricto: *V. infundibulum* (Philippi 1844), Mediterranean; *V. richardi* Fauvel 1909, Mediterranean; *V. monodiscus* Zibrowius 1968b, Mediterranean.

Pseudovermilia Bush 1907b; emended Zibrowius 1970

Type-species — *Spirobranchus occidentalis* McIntosh 1885, by original designation. Gender: female.

The following species is referred to *Pseudovermilia* (see Zibrowius 1968a p. 120; 1970 p. 126–127): *P. occidentalis* (McIntosh 1885), Bermuda. Synonyms: *Vermilia nigropileata* Ehlers 1900, Patagonia; *Pseudovermilia pileum* Bush 1907b, Bermuda; *Pomatostegus galeatus* Fauvel 1909, Cape Verde Islands; *Vermiliopsis cornuta* Rioja 1947, Mexico (Pacific coast); *P. multispinosa* (Monro 1933), Columbia (Pacific coast). The species described as *Crosslandiella multispinosa* Monro 1933 (holotype examined, BMNH) has a distally enlarged thick (not flat ribbonlike) opercular stalk; all other characters are those of *Pseudovermilia*.

Metavermilia Bush 1904; emended

Type-species — *Vermilia multicristata* Philippi 1844, by original designation. Mediterranean. Gender: feminine.

Diagnosis — Tube white, not transparent, irregularly sinuous or coiled. Operculum with horny, noncalcified terminal structure. Opercular stalk flat, large, ribbonlike, formed from second dorsal filament on one side. No pseudo-operculum, no gill membranes. Thoracic membranes extending more or less far posteriorly, sometimes possibly united ventrally on posterior thoracic segment. Thoracic setigerous segments 7, 6 of them uncinigerous. Setae of anterior thoracic segment ("collar setae") similar to those of following segments (no special setae). Three kinds of thoracic setae: (1) more or less limbate; (2) capillary; (3) sickle-shaped, with denticulate inner margin and small proximal limbate zone. Abdominal setae more or less geniculate or rather straight; capillary setae in posterior segments. Thoracic uncini saw-shaped; abdominal uncini saw-shaped or rasp-shaped; anterior tooth simple (not bifurcate).

The following species are referred herein to *Metavermilia*: *M. multicristata* (Philippi 1844), Mediterranean and northeast Atlantic between Gulf of Guinea, Azores, and Gulf of Biscay; *M. annobonensis* new species, Annobon, Gulf of Guinea; *M. taenia* new species, Josephine Bank, northeast Atlantic off Portugal; *M. nates* new species, Europa Island, Mozambique Channel, and Tanzania coast.

The species from California described by Moore (1923 p. 251–253, pl. 18, fig. 48), as *Metavermilia multiannulata*, with a simple, not ribbonlike opercular stalk, appears to be a species of *Vermiliopsis* sensu stricto and closely allied to the Mediterranean *V. infundibulum* (Philippi). However, Hartman (1969 p. 781–782, fig. 1, under the name of *Vermiliopsis multiannulata*) apparently confused a species of *Pseudovermilia* with Moore's species; the figure of the operculum is similar to that shown by Rioja (1947) for *Vermiliopsis cornuta*.

The most characteristic structure of *Metavermilia* (not previously emphasized in the descriptions of the type species) is that of the opercular stalk, being flat and ribbonlike and formed from the second dorsal filament on one side (not the most dorsal); in addition, the general types of setae and uncini are the same. However, in the matter of the detailed

structure of the setae and uncini, as well as of the configuration of the thoracic membranes, the four species referred herein to *Metavermilia* are more diversified than most other generally accepted genera.

In former publications (Zibrowius 1968a etc.), it was suggested that the presence of rasp-shaped uncini in all abdominal segments was of prime importance for generic classification. Indeed, the structure of abdominal uncini may reveal or confirm close relationship between species, but it appears now that this character is not an absolute one and not necessarily of prime importance in all genera. Rasp-shaped uncini are always found in the most posterior segments, and thus the youngest, of even those species that, in more anterior abdominal segments, have saw-shaped uncini. With further growth of the worm, these posterior segments are found farther and farther away from the pygidium, and the rasp-shaped uncini are replaced by sawshaped ones. The same should be said of the importance of the thoracic membranes for classification. They surely can often provide useful characters but not necessarily of prime importance when other very particular structures are common to species differing by details of the thoracic membranes.

The diagnosis of the genus *Metavermilia* Bush (herein revalidated and emended) should thus emphasize the particular structure and position of the opercular stalk rather than insist on close resemblance with the type-species (*M. multicristata*) in details of setae, uncini, and thoracic membranes.

Metavermilia multicristata (Philippi)

Fig. 1

Vermilia multicristata Philippi 1844, p. 193, pl. 6, fig. K (Mediterranean, southern Italy).

Serpula sulcosa Costa 1861, p. 33, pl. 7, fig. 5 (Mediterranean, southern Italy).

Vermilia clavigera — Langerhans 1884, p. 279–280, pl. 17, fig. 42*a–b* (Madeira). Not Philippi 1844.

Vermilia multicostata — Langerhans 1884, p. 280, pl. 17, fig. 43 (Madeira). (Error for *multicristata*.)

Vermilia multicristata — Marenzeller 1893, p. 41, pl. 4, fig. 14 (eastern Mediterranean; synonymy).

Vermiliopsis multicristata — Fauvel 1909, p. 60–61, 1914, p. 344 (Azores; material studied, MOM); 1927, p. 365–366, fig. 125*k–s* (no new records); 1936, p. 113 (Morroco, in part??; not station 83; = *Omphalopomosis fimbriata* (Delle Chiaje); material studied, MNHN). Fauvel and Rullier 1957, p. 390–391 (Senegal); 1959, p. 984 (Senegal). Bellan 1959, p. 339 (Gorringe Bank). Southward 1963, p. 584 (continental slope off Britany). Rullier 1964, p. 206 (Cape Verde Islands; material studied, MNHN). Zibrowius 1968a, p. 128–130, pl. 3, fig. 25–34, pl. 14, fig. *g* (northwest Mediterranean and new record from Gulf of Biscay); 1968c, p. 377 (Madeira); 1969b, p. 129 (Tunisia); 1970, p. 121 (Portugal and Josephine Bank). Uschakov 1970, p. 454 (Guinea).

Not *Vermiliopsis multicristata*? — Monro 1937, p. 319 (Tanzania coast; = *Metavermilia nates* new species).

Not *Vermiliopsis multicristata* — Tebble 1955, p. 145–146 (Ghana; = *Vermiliopsis* sp., sensu stricto, material studied, BMNH). Kirkegaard 1959, p. 106–107 (Canary Islands; = *Vermiliopsis* sp., sensu stricto, material studied, ZMC).

Material studied — Numerous specimens from various areas of the Mediterranean (Marseilles, Port Cros, Villefranche, Tyrrhenian Sea, Tunisia, Lybia, Bari, Creta — author's personal collection) and the Atlantic (Azores, Gulf of Biscay, Portugal, Josephine Bank, Madeira, Canary Islands, Cape Verde Islands, Annobon — author's collection, MOM, MNHN), including new records from: (*a*) Prince of Monaco expeditions (MOM): station 1121, July 12, 1901, Canary Islands, 28°47′N, 13°44′45″W, 540 m; station 1242, September 10, 1901, Seine Bank, 1 mile east of 33°45′N, 14°20′15″W, 240 m; station 1304, July 27, 1902, Josephine Bank, 36°41′N, 14°11′45″W, 208 m; station 1463, July 27, 1903, Gulf of Biscay, 45°20′N, 3°17′W to 45°24′N, 3°07′W, 932–150 m. (*b*) "Jean Charcot" cruise "Noratlante" 1969 (author's collection): P.71/E.9, October 9, 1969, Josephine Bank, 36°40′4″N, 14°15′6″W, 215 m; P.72/E.10, October 9, 1969, Josephine Bank, 36°39′1″N, 14°13′W, 690 m; P.76/D.8, October 10, 1969, Gorringe Bank, 36°34′9″N, 11°38′2″W, 600 m. (*c*) Gulf of Guinea (author's collection): OM.29, December 11, 1965, Annobon, drag. 3, 1°25′24″S, 5°39′E, 52 m.

Description — Tube white, not transparent, rather thin-walled and circular in cross-section, not encrusting the substrate, with 5–7 longitudinal keels and some transverse ridges; distal part sometimes slightly detached from substrate and orifice slightly widened out into simple funnel-shaped peristome. Keels of tube either smooth ridges or high thin crests divided into numerous brittle teeth; median keel on upper face slightly less developed than other upper keels.

Total length of worms up to 10 mm, operculum up to 0.90 mm in diameter, abdominal segments about 60, about 10–12 branchial filaments on each side in large specimens; living specimens generally with several large red spots on branchial filaments, gill tuft then appearing annulated. Prostomium with one pair of red (ocular?) spots.

Collar divided into three principal lobes: ventral lobe sometimes notched in midventral line, with small secondary lobe; laterodorsal lobes continuous with long thoracic membranes, merging into midventral "apron" on posterior thoracic segment; constriction of thoracic membranes sometimes present at about segment 3.

Branchial filaments arranged in semicircles and ending in terminal filaments similar to pinnules; without basal membranes uniting filaments. No small distinct crystalline pyriform structures observed in axes of filaments. Second dorsal filament on left or on right side trans-

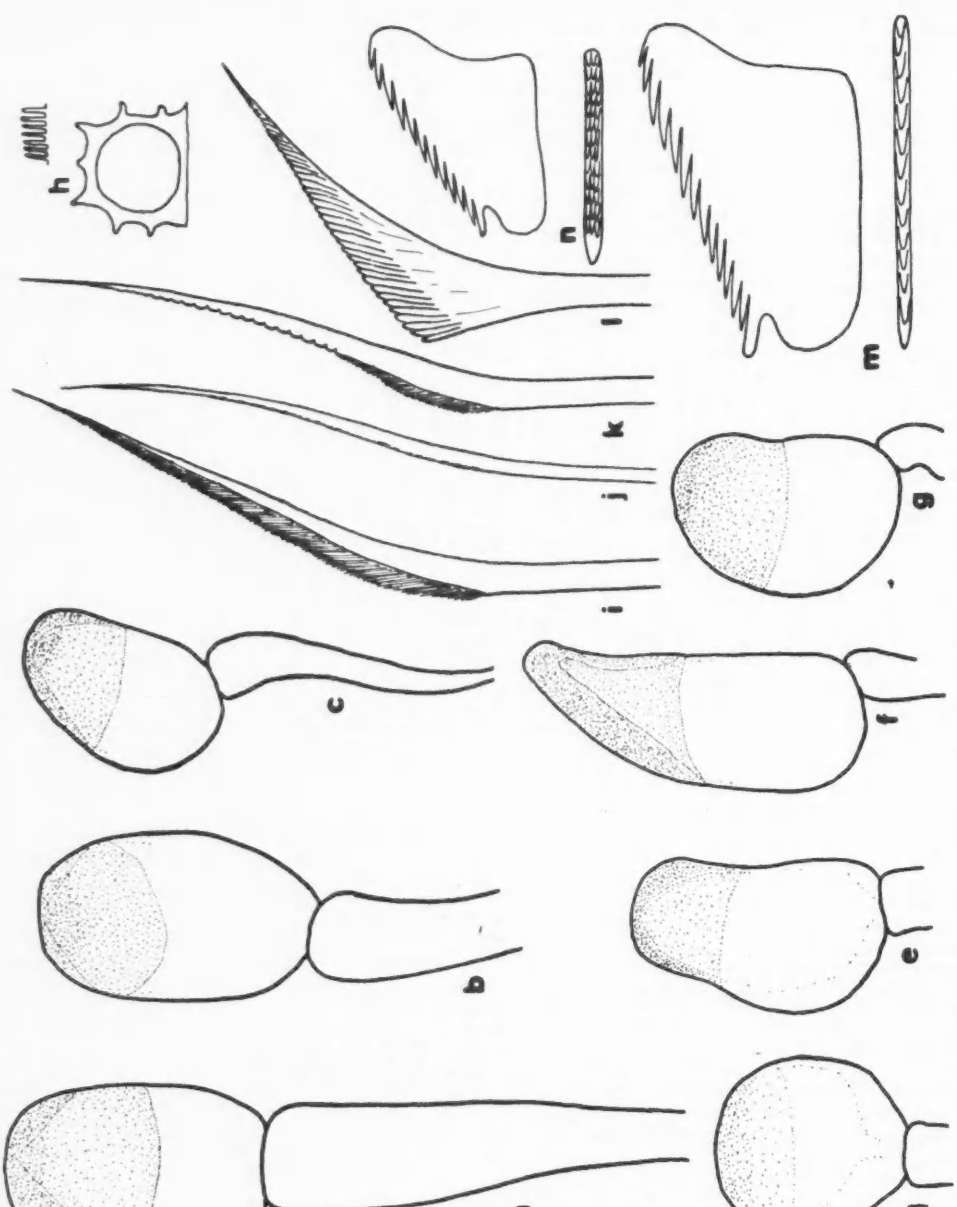

FIG. 1. *Metavermilia multicristata* (specimens from Marseille area, northwest Mediterranean): *a–g*, various views of opercula; *h*, schematic cross section of tube and part of finely denticulate crest; *i*, *j*, setae from first thoracic segment; *k*, thoracic sickle seta ("*Apomatus* seta"); l, abdominal geniculate seta; *m*, thoracic uncinus, side and end views; *n*, abdominal uncinus, side and end views.

formed into large ribbonlike opercular stalk (at least half as large as operculum).

Operculum with well-marked bilateral symmetry (dorsal side rather straight, ventral side bulging); opercular stalk attached to dorsal side. Lower part of operculum soft, vesicular, upper part hemispherical, forming more or less elongate horny cap, smooth, simple, not subdivided, yellowish or brown, without any calcareous deposit, hollow (interior continuous with lower soft part) but sometimes very thick-walled.

Setae of first thoracic segment less numerous than those of following segments but similar and of same size (capillary and limbate setae); sickle-shaped setae ("*Apomatus* setae") with denticulate blade and short proximal limbate zone, present in segments 3–7. Abdominal setae geniculate, with triangular denticulate blade; these setae replaced by long slender capillary setae in most posterior segments.

Thoracic uncini with about 11–15 teeth in one row on free margin (saw-shaped uncini); anterior tooth simple (not bifurcate), rather slender and slightly curved upward. Abdominal uncini similar in form though more curved, but in all segments with several rows of teeth (rasp-shaped uncini).

Remarks — Philippi's original description was based on a single dry specimen from southern Italy (material lost) but the tube and operculum were rather well characterized. Under the name *Serpula sulcosa* (synonymy here reported for the first time), Costa (1861) described and figured a tube of the same species from southern Italy. Marenzeller (1893) gave a detailed and well-illustrated description (except for the ribbonlike opercular stalk not well observed), based on material from several localities in the eastern Mediterranean. Marenzeller, having studied Langerhans' (1884) original material from Madeira, identified as *Vermilia clavigera* (a poorly described species of Philippi 1844) and *Vermilia multicostata* (error for *V. multicristata*), found them to be *Vermilia multicristata*.

Subsequently, the species was reported from various areas of the Mediterranean (as *Vermiliopsis multicristata*; see Zibrowius 1968a, 1969b) and the Atlantic (see synonymy above). Some of these records should be checked. Though material from Morroco, the Canary Islands, and the Gulf of Guinea (Ghana), reported as *Vermiliopsis multicristata* (Philippi), proved to belong to other species, the above indicated geographical range (northeast Atlantic between Gulf of Guinea, Azores, and Gulf of Biscay) remains essentially correct, as confirmed by the new records. Up to now, *M. multicristata* has not been found in the Indian Ocean. In the Mediterranean it was found from very shallow water down to depths of several hundred meters; its bathymetrical range in the northeast Atlantic is similar.

Metavermilia multicristata is a species quite common in the Atlantic. Fauvel (1909, 1914) reported it from a single station of the Prince of Monaco expeditions, but recently, when studying various substrates encrusted by serpulids (scleractinian corals, shells, etc. collected during these expeditions, MOM), it was found that the species had been collected in several other stations (see above). Additional specimens were obtained by the "Jean Charcot" 1969 North Atlantic cruise ("Noratlante") and from the Gulf of Guinea.

Metavermilia annobonensis n.sp.
Fig. 2

Material studied — Annobon, Gulf of Guinea, 1°25′24″S, 5°39′E, 52 m, on lower face of clump of *Madracis decactis* (Lyman) and calcareous algae (cruise Ombango 29, drag. 3, December 11, 1965). Holotype (USNM 44066).

Description — Tube white, not transparent, attached to substrate throughout its length, subquadrangular in cross section, with several (4–6) longitudinal irregular keels (not denticulate), four most distinct keels on upper side; orifice forming simple flared peristome with thin irregular margin.

Total length of worm 16 mm (including 3 mm for gill tuft), operculum 0.62 mm in diameter, about 80 abdominal segments, 9 branchial filaments on each side. Prostomium with one pair of lateral pigmented (ocular?) spots; preserved specimen otherwise not pigmented except for spots of white pigment on branchial filaments. Collar divided into three lobes, laterodorsal ones continuous with thoracic membranes, being large at least up to thoracic segments 3–4.

Branchial filaments arranged in semicircles and ending distally in simple tips similar to pinnules; without basal membranes uniting filaments. Axes of filaments with two series of small distinct pyriform crystalline structures, not pigmented on preserved material (refracting cells of ocellae?). Second dorsal filament on right side transformed into flat ribbonlike opercular stalk, as large as operculum distally.

Operculum with well-marked bilateral symmetry (dorsal side rather straight, ventral side bulging) ending in simple concave distal plate, being rather thick and brown, without calcareous deposit.

Setae of first thoracic segment less numerous than those of following segments but similar and of same size (capillary and limbate setae); sickle-shaped setae ("*Apomatus* setae") with denticulate blade and small proximal limbate zone, present in thoracic segments 3–7. Abdominal setae geniculate, with triangular denticulate blade; these setae replaced by long capillary setae in most posterior segments.

Thoracic uncini with about 7 teeth in one row on free margin (saw-shaped uncini); anterior tooth simple (not bifurcate). Abdominal uncini similar to thoracic ones,

geniculate seta; *m*, thoracic uncinus, side and end views; *n*, abdominal uncinus, side and end views.

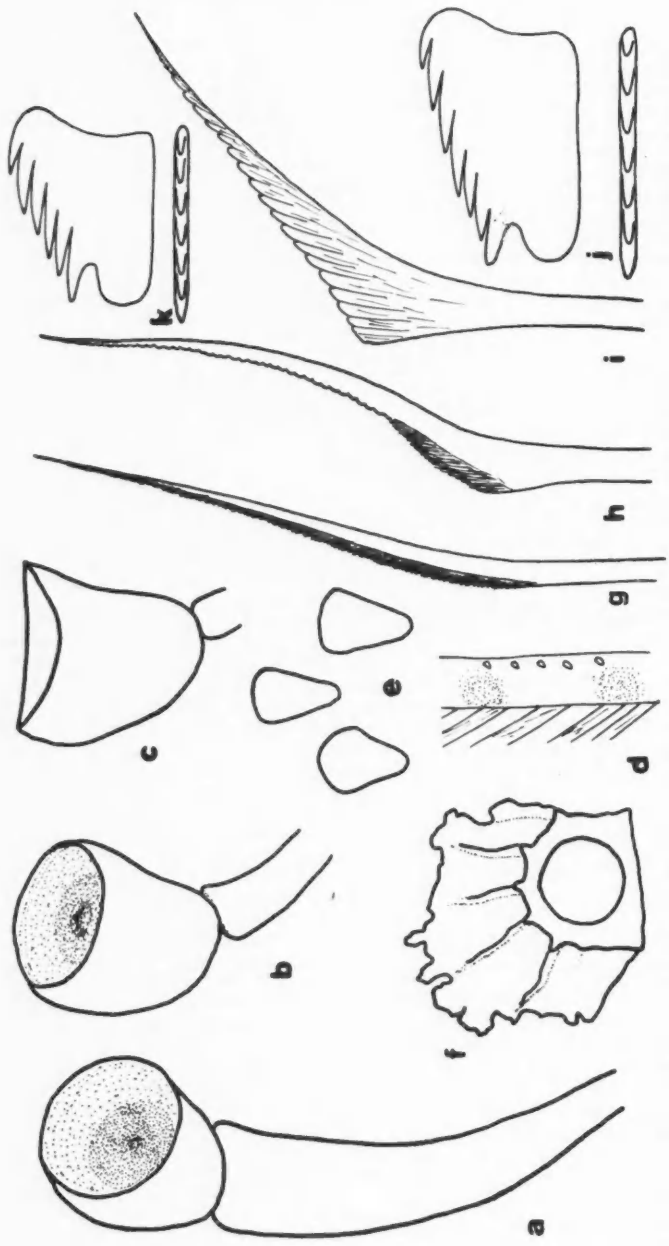

FIG. 2. *Metavermilia annobonensis* n.sp. (holotype): *a, b,* two views of operculum; *c,* schematic section of same; *d,* part of branchial filament showing distinct pyriform structures in axis, schematic view; *e,* pyriform structures from axis of branchial filament; *f,* cross section of distal part of tube, enlarged towards orifice, *g,* thoracic limbate seta; *h,* thoracic sickle seta ("*Apomatus* seta"); *i,* abdominal geniculate seta; *j,* thoracic uncinus, side and end views; *k,* abdominal uncinus, side and end views.

saw-shaped in all segments except in very few posterior ones where uncini furnished with several rows of teeth (rasp-shaped uncini).

Remarks — *Metavermilia annobonensis* is well characterized by its uncini with rather few teeth and its operculum with a simple concave distal plate. Similar to *M. multicristata*, *M. annobonensis* has a pair of pigmented spots on the prostomium. It has branchial filaments with small distinct crystalline pyriform structures, similar to *M. nates*. The tube resembles more closely that of *M. multicristata* than those of the other species of *Metavermilia* here described.

Metavermilia taenia n.sp.
Fig. 3

Material studied — Josephine Bank, northeast Atlantic off Portugal, "Jean Charcot" (cruise "Noratlante"), P.72/E.10, October 9, 1969, 36°39′N, 14°13′W, 690 m, on lower side of slab of calcareous sandstone. Holotype (USNM 44068).

Description — Tube white, not transparent, forming several piled-up whorls; cross section semicircular, with encrusting base; surface smooth except for transverse ridges (no longitudinal keels); walls thick and solid, as thick as aperture.

Total length of worm about 16 mm (including 6 mm for gill tuft), operculum 1.35 mm in diameter, about 80 abdominal segments; about 16 or 17 branchial filaments on each side. Preserved specimen without pigmentation. Collar divided into three lobes, laterodorsal ones continuous with long thoracic membranes, being large throughout all thoracic segments but not merging in midventral "apron" on posterior thoracic segment (rows of uncini of posterior thoracic segments similar to those of anterior ones).

Branchial filaments ending distally in simple tips similar to pinnules; no basal membranes uniting filaments; no small crystalline pyriform structures observed in axes of filaments. Second dorsal filament on right side transformed into large flat, ribbonlike opercular stalk, more than half as large as operculum distally.

Operculum with bilateral symmetry (insertion of opercular stalk on dorsal side), ending in thin-walled, almost hemispherical horny cap without any calcareous deposit, black and smooth, simple, not subdivided.

Setae of first thoracic segment less numerous than those of following segments but similar and of same size (very slender tapering capillary and limbate setae); almost straight "sickle" setae ("*Apomatus* setae") with denticulate blade and slightly limbate proximal zone, present at least in thoracic segments 4–7. Abdominal setae almost straight, with elongate narrow blade, hardly geniculate; these setae replaced by long capillary setae in most posterior segments (about 18 segments).

Thoracic uncini with about 11 teeth in one row on free margin (saw-shaped uncini); anterior tooth simple (not bifurcate). Abdominal uncini similar to thoracic ones, saw-shaped in all segments except in very few

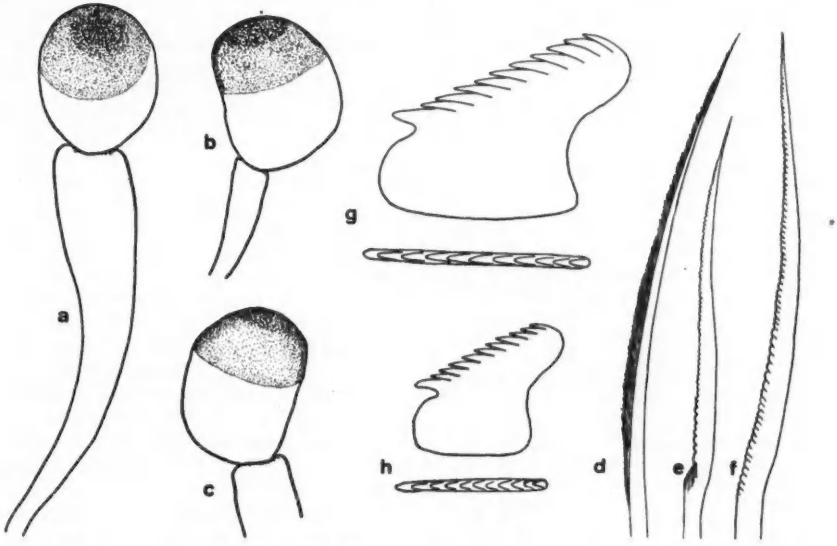

FIG. 3. *Metavermilia taenia* n.sp. (holotype): *a–c*, three views of operculum; *d*, thoracic limbate seta; *e*, thoracic sickle seta ("*Apomatus* seta"); *f*, abdominal seta; *g*, thoracic uncinus, side and end views; *h*, abdominal uncinus, side and end views.

posterior segments where uncini furnished with several rows of teeth (rasp-shaped uncini).

Remarks — *Metavermilia taenia* shows some very particular specific characters: tube smooth and very thick-walled; operculum with black horny cap; thoracic setae particularly slender and tapering; thoracic "sickle" setae and abdominal setae rather straight.

Mevermilia nates n.sp.

Fig. 4

Vermiliopsis multicristata? — Monro 1937, p. 319 (Tanzania coast).

Material studied — Europa Island, Mozambique Channel, coll. P. Vasseur, P.5, December 25, 1965, Bay Gabriel, north reef (lee side), seaward slope, 40 m, on *Distichopora* sp. Holotype (USNM 44067). Tanzania coast opposite Pemba, John Murray Expedition, station 112, January 15, 1934, 5°04′57″S, 39°13′18″E, 113 m, on spine of Cidaridae. Paratype (BMNH 1937.9.2.575).

Description — Tube white, not transparent, with several crests or keels, attached to substrate throughout its length. Tube of larger specimen (holotype) almost triangular in cross section (up to 2.4 mm wide), with high median crest with irregular margin (not regularly denticulate) and two less-developed keels on each side, with laterally compressed triangular or more irregularly formed teeth. Tube of smaller specimen (paratype) semicircular in cross section, with up to 9 more-or-less developed, irregularly denticulate crests or keels: 3 poorly developed keels on upper face, 2 well-developed high crests, and 2 or 4 slightly developed lateral keels.

Anterior part of both holotype and paratype somewhat incomplete (thoracic membranes damaged, setae of first segment broken away). Preserved material without any pigmentation. Holotype from Europa Island: total length 25 mm, operculum 1.35 mm in diameter; abdominal segments about 80; about 20 branchial filaments on each side. Paratype from Tanzania coast: total length 15 mm; operculum 0.90 mm in diameter, about 15 branchial filaments on each side. Details of collar structure unknown. Thoracic membranes apparently large, extending up to last thoracic segment and possibly merging into midventral "apron" (rows of uncini becoming shorter in posterior thoracic segments, similar to *M. multicristata* and to species of other genera with ventrally merging thoracic membranes).

Branchial filaments arranged in spirals of up to 1.5 whorls; no basal membranes uniting filaments; all filaments ending distally in enlarged clavate tips, very unlike pinnules or filaments in other species of *Metavermilia*. Axes of branchial filaments with two series of isolated small crystalline pyriform structures (refracting cells of ocellae?). Second dorsal filament on left side transformed into large flat, ribbonlike opercular stalk, being as large as operculum distally.

Operculum with bilateral symmetry and differentiated into two distinct parts: proximal soft part, vesicular and globular; and distal horny part, yellow-brown, composed of several similar pieces forming set of radially striated disks widened out from lower cylindrical parts or of more funnel-shaped pieces; disks or funnels with entire margins except middorsally with margin depressed and notched, especially in lower ones. Base of lowest piece (biggest and youngest) continuous with soft globular part of operculum. Soft globular part of operculum on holotype (bigger specimen) with deep furrow middorsally in line with series of notches of horny disks; furrow separating two bulging smooth zones. Operculum of paratype (smaller specimen) with lower part quite regularly shaped and smooth, without any furrow.

Setae of first thoracic segment broken away distally in both specimens, unknown. Following uncinigerous segments 2–7 with capillary and limbate setae; sickle-shaped setae ("*Apomatus* setae") present at least in posterior thoracic segments (observed on holotype, not on paratype with most of setae broken away distally). Abdominal setae geniculate with rather long and narrow triangular blade, being replaced by long capillary setae in 15–20 posterior segments.

Thoracic uncini with about 8–10 teeth in one row on free margin (saw-shaped uncini); anterior tooth simple (not bifurcate). Abdominal uncini similar to thoracic ones, saw-shaped in all segments except in very few (about 3) posterior segments provided with uncini with several rows of teeth (rasp-shaped uncini); uncini of most anterior segments with 6–7 teeth; more posterior uncini with same number of teeth as thoracic ones.

Remarks — *Metavermilia nates* is characterized by its opercular structure (distal horny part); however, the furrow observed on the lower soft part of the holotype (not observed on the paratype) may be due to a mutilation and thus not a specific character. The enlarged distal tips of the branchial filaments appear to be another specific character (similar structures described for *Filograna huxleyi* Ehlers 1887). Similar to *M. annobonensis*, *M. nates* has branchial filaments with small crystalline pyriform structures. When Monro (1937) referred, with doubts, the first specimen collected of *M. nates* to *M. multicristata* (as *Vermiliopsis*), he took into account only a very superficial resemblance with the latter species that was known to him only by literature (tube with several denticulate crests). As the setae of the first thoracic segment are still unknown, the generic position of *M. nates* should be confirmed by examination of additional more complete specimens.

In regard to the operculum, *M. nates* shows some resemblance to *Vermiliopsis pomatostegoides* Zibrowius, as well as to *Pomatostegus stellatus* (Abildgaard). All three species are characterized by the horny parts of their opercula composed of a set

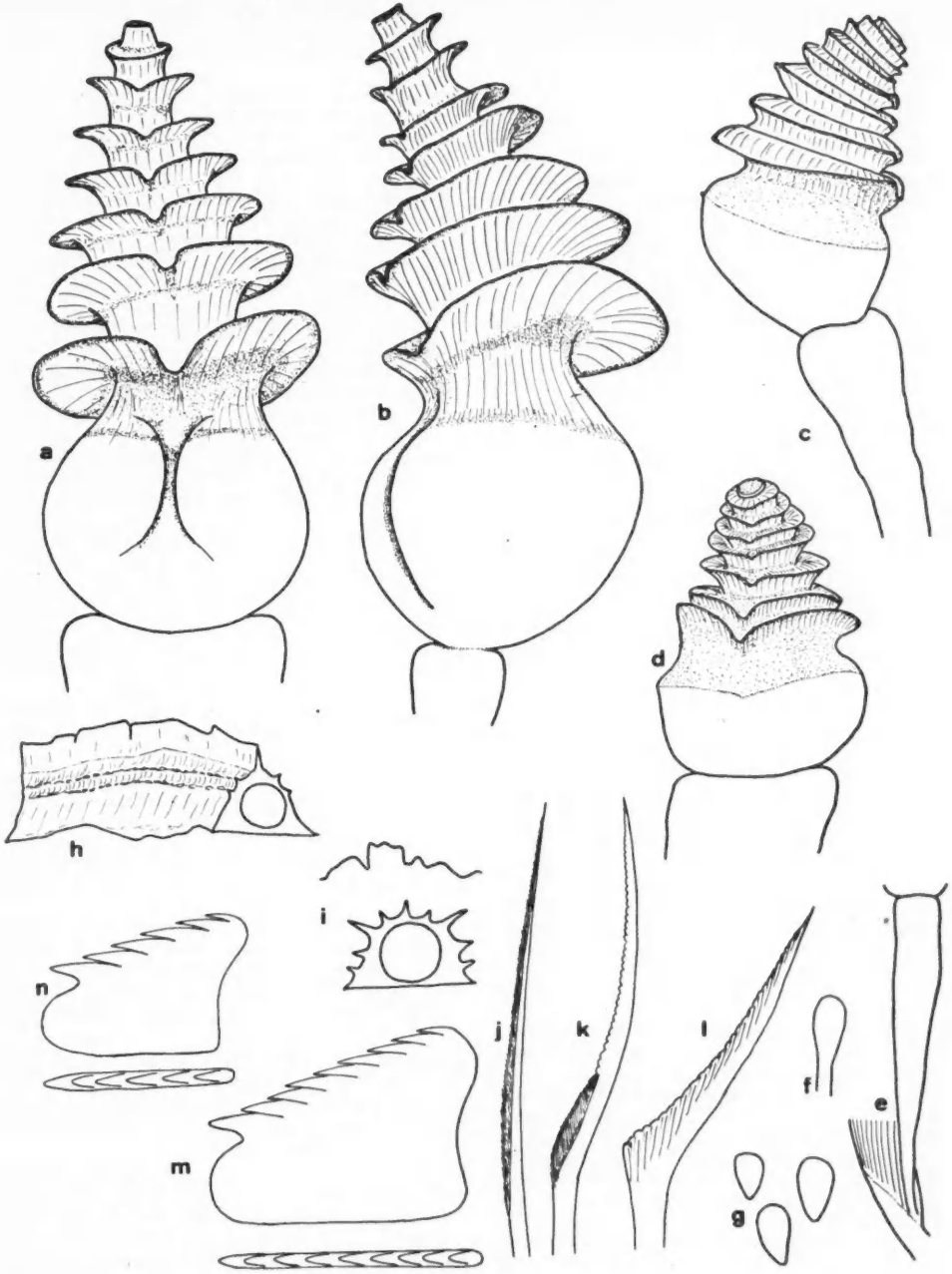

FIG. 4. *Metavermilia nates* n.sp. (*a*, *b*, *e–h*, *j–n*, holotype; *c*, *d*, *i*, paratype): *a*, *b*, two views of operculum; *c*, *d*, two views of operculum; *e*, schematic view of left side of branchial crown base, second dorsal filament forming opercular stalk; *f*, enlarged distal tip of branchial filament; *g*, pyriform structures from axis of branchial filament; *h*, tube; *i*, schematic cross section of tube and irregular denticulate margin of keel; *j*, thoracic limbate seta; *k*, thoracic sickle seta ("*Apomatus* seta"); *l*, abdominal geniculate seta; *m*, thoracic uncinus, side and end views; *n*, abdominal uncinus, side and end views.

of similar pieces. In *V. pomatostegoides* (*Vermiliopsis* sensu lato), a small species from the southern Mediterranean, the horny disks, separated by simple cylindrical pieces, are smooth with entire margins; the species, with a simple cylindrical opercular stalk is characterized by its wide thick-walled tube. In *P. stellatus*, a world-wide species from tropical seas (abundant material studied, chiefly USNM and BMNH, from various localities in the Atlantic, Indian, and Pacific oceans), the horny opercular disks have a more-or-less serrated margin and are separated by very slender cylindrical pieces and crowns of spines; the lower soft part of the operculum is flattened, and the opercular stalk has large wings ending distally in triangular lobes (very unlike *M. nates*); this large species has special setae in the first thoracic segment; otherwise its setae and uncini are similar to those of *M. nates*.

Remarks on parasites — It should be noted here that numerous small undoubtedly parasitic organisms of uncertain systematic position are solidly attached to most of the branchial filaments of the paratype of *M. nates* (BMNH 1937.9.2.575). These organisms, up to 0.15 mm long, are compressed laterally, and attached to the axes of the filaments by a slender peduncle. This seems to be a new form of parasitism in serpulid polychaetes.

Acknowledgments

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Polychaetes as Intermediate Hosts of Helminth Parasites of Vertebrates: A Review

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MARGOLIS, L. 1971. Polychaetes as intermediate hosts of helminth parasites of vertebrates: a review. J. Fish. Res. Bd. Canada 28: 1385–1392.

The role of polychaetes as intermediate hosts of helminth parasites of aquatic vertebrates is reviewed. Some 18–20 species of trematodes and three or four each of cestodes and nematodes are known to have larval stages in these annelids. There are no records of acanthocephalan larvae from polychaetes. Trematoda use polychaetes as first (three species) or second intermediate hosts. The polychaete hosts are found among various genera of Errantia, Sedentaria, and Myzostomida. Definitive hosts are mainly fishes, with a few species of trematodes and one of cestodes developing in birds, and apparently one genus of nematodes (two species) maturing in the lungs of seals. A list of polychaetes and their larval helminth parasites is given.

MARGOLIS, L. 1971. Polychaetes as intermediate hosts of helminth parasites of vertebrates: a review. J. Fish. Res. Bd. Canada 28: 1385–1392.

L'auteur passe en revue le rôle des polychètes en tant qu'hôtes d'helminthes parasites des vertébrés aquatiques. De 18 à 20 espèces de trématodes, trois ou quatre espèces de cestodes et autant de nématodes sont, à l'état larvaire, parasites de ces annélides. On n'a pas trouvé de larves d'acanthocéphales chez les polychètes. Les trématodes se servent de polychètes comme hôtes intermédiaires primaires (trois espèces) ou secondaires. Les polychètes infestés se rencontrent parmi divers genres d'Errantia, Sedentaria et Myzostomida. Les hôtes définitifs sont surtout des poissons, bien que quelques espèces de trématodes et une de cestodes se trouvent dans des oiseaux, et un genre de nématodes (deux espèces) se développe dans le poumon des phoques. L'auteur dresse une liste des polychètes et de leurs helminthes larvaires parasites.

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OF the four major groups of endoparasitic helminths of vertebrates, the representatives of three (Trematoda, Cestoidea, Acanthocephala) regularly (except for the rodent cestode *Hymenolepis nana*) undergo a period of development in one or more hosts other than the vertebrate host in which they reach maturity. Many members of the fourth group, the Nematoda, have a similar life-history pattern. Various invertebrates or, less frequently, vertebrates, serve as intermediate hosts, a particular set of hosts being more or less characteristic for each species of helminth.

For a number of helminths reaching sexual maturity in aquatic vertebrates, polychaetous annelids are used as intermediate hosts. In this paper the role of polychaetes in the life of helminths parasitic in aquatic vertebrates will be reviewed.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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Trematoda

POLYCHAETES AS FIRST INTERMEDIATE HOSTS

The life cycle of digenetic trematodes or Digenea typically involves a mollusc as the first intermediate host, in which cercariae, infective for the next host in the life cycle, develop. The only known exceptions to this general rule are provided by three species of trematodes in which cercarial development occurs in the coelom of sedentary, tube-dwelling polychaetes. One species, *Cercaria loossi* develops in *Hydroides dianthus* in the Woods Hole area, eastern seaboard of the USA (Linton 1915; Stunkard 1929; Martin 1944; Rankin 1946); another, *Cercaria hartmanae*, occurs in *Lanicides vayssierei* at Ross Island in the Antarctic (Martin

1952); and the third, *Cercaria amphicteis*, was described from *Amphicteis gunneri floridus* in the Apalachicola River estuary, northwestern Florida (Oglesby 1961). The adults of these three trematodes are unknown. Their polychaete hosts are members of three different but closely related families — Serpulidae, Terebellidae, and Ampharetidae.

The three cercariae are of the apharyngeate monostome type and are thought to belong to the Sanguinicolidae (syn. Aporocotylidae), a family of trematodes inhabiting the vascular system of fishes. Other similar marine cercariae are known to develop in bivalve molluscs (Oglesby 1961) and species of Sanguinicolidae from freshwater fishes use gastropod molluscs as first intermediate hosts. The evolutionary significance of the replacement of the usual molluscan host with a polychaete and the evolutionary process by which this occurred are not obvious.

Of the three cercariae that develop in polychaetes, most is known about *C. loossi*. Apparently it is specific for *Hydroides dianthus*. Rankin (1946) examined 15 species of tube-dwelling polychaetes from the Woods Hole area and found *C. loossi* only in *H. dianthus*. Thus, the host specificity usually exhibited by trematodes for their molluscan hosts appears also to be a characteristic of the species using polychaetes as their first intermediate hosts.

Martin (1944) observed that sporocysts containing the cercariae of *C. loossi* leave the polychaete host through lateral pores along each side of the body, which are also used for the discharge of the host's genital products. The cercariae are released upon rupture of the sporocysts in the water. Presumably the water current created by movement of cilia on the ventral surface of the polychaete sweeps the sporocysts and cercariae out of the host's tube. The free-swimming cercariae may then infect the next host, in this instance (judging from known life-cycle patterns in blood flukes) probably the definitive fish host.

Polychaetes as Second Intermediate Hosts

Most digenetic trematodes of aquatic vertebrates have a three-host life cycle. Between the usual molluscan first intermediate host and the vertebrate definitive host there is interposed a second intermediate host, which may be an invertebrate or a lower vertebrate. The cercariae produced in the mollusc are ingested by or actively penetrate the second intermediate host and develop to the metacercarial stage. Depending upon the species of trematode, the metacercariae may encyst in tissues or exist free in cavities of the second intermediate host. Infection of the definitive host occurs through ingestion of metacercariae in the second intermediate host.

At least a dozen trematode species found in fishes, and three or four species parasitic in birds, use or are known to be able to use polychaetes as second intermediate hosts (Table 1). Of the species listed in Table 1, those belonging to the families Didymozoidae, Fellodistomatidae, Hemiuridae, Lepocreadiidae, Monorchiidae, and Zoogonidae use fishes as definitive hosts; those belonging to the Echinostomidae and Gymnophallidae use birds as definitive hosts. The definitive hosts of the undetermined group listed in Table 1 are unknown, although Stunkard (1950) believed *Cercaria parvicaudata* to be a member of the Plagiorchiidae that matures in birds or mammals.

Usually, only single-species infections of individual polychaetes have been reported, but Timon-David and Rebecq (1958) and Rebecq (1964) have noted as many as three species (*Gymnophallus nereicola*, *Himasthla militaris*, and *Deropristis inflata*) occurring simultaneously in *Nereis diversicolor* from the Mediterranean coast of France.

Judging from statements made by Caullery and Mesnil (1900), one may expect the number of trematodes using polychaetes as second intermediate hosts to be greater than that shown in Table 1, with more species of polychaetes being involved. Caullery and Mesnil, who made observations on parasites of polychaetes in the waters around France, stated: "Les Trématodes sont représentés par de très nombreuses larves de Distomes enkystées et provenant de Cercaires. On en trouve dans la cavité générale de presque toutes les Annélides marines. Nous en avons vu chez divers Cirratuliens, Spionidiens, Serpuliens, etc., etc."

For some of the digeneans listed in Table 1, polychaetes are the only known second intermediate hosts, in some instances only one or a few closely related species being suitable, whereas, for others, the range of second intermediate hosts includes other invertebrates as well. Some of the records are based only on experimental infections (see Table 1) and for these it is not known if polychaetes are natural hosts.

Examples of species using only polychaetes are *Deropristis inflata*, *Gymnophallus nereicola*, *Zoogonoides laevis*, and *Zoogonus lasius*. The metacercariae of the last two are known to develop only in *Nereis virens*. (Other species of *Nereis* have not been tested.) Stunkard (1943) attempted to infect a number of invertebrates including molluscs, crustaceans, and "worms" by exposing them to cercariae of *Z. laevis*; only *N. virens* became infected. In experiments with *Z. lasius*,

TABLE 1. List of trematodes using polychaetes as second intermediate hosts.[a]

Trematodes	Polychaetes	Locality	References
Didymozoidae gen. et spec. indet.	*Tomopteris helgolandica*	Baltic Sea	Reimer pers. commun.
Fellodistomatidae			
Proctoeces maculatus	*Nereis caudata, Hydroides norvegica*	Mediterranean (France)	Prévot 1965
Hemiuridae			
Derogenes varicus	*Harmothoe imbricata*	Greenland	Levinsen 1881; Ditlevsen 1914
Gen. et spec. indet.	*Tomopteris vitrina*	Adriatic (Trieste)	Mrázek 1917
Lepocreadiidae			
Depropristis inflata	*Nereis diversicolor, Platynereis dumerili*	Mediterranean (France)	Carrère 1937; Timon-David and Rebecq 1958; Rebecq 1964
Depropristis inflata	*Nereis virens*	Woods Hole, Mass. (USA)	Cable and Hunninen 1942
Homalometron pallidum	Unidentified "small polychaetes"[b]	Woods Hole, Mass. (USA)	Stunkard 1964
Lepidapedon gadi	*Harmothoe imbricata, Lepidonotus squamatus, Nereis pelagica*	Barents Sea	Amosova 1955
Lepocreadium album	*Alciope* sp.	?	Fuhrmann 1928
Lepocreadium setiferoides	*Spio* sp.[b]	Woods Hole, Mass. (USA)	Martin 1938
Opechona bacillaris	*Tomopteris helgolandica*	Baltic Sea	Reimer pers. commun.
Monorchiidae			
Asymphylodora demeli	*Alkmaria romijni, Nereis diversicolor*	Baltic Sea	Reimer 1970, pers. commun.
Zoogonidae			
Zoogonoides laevis	*Nereis virens*[b]	Woods Hole, Mass. (USA)	Stunkard 1943
Zoogonus lasius	*Nereis virens*[c]	Woods Hole, Mass. (USA)	Shaw 1933; Stunkard 1938, 1941
Echinostomatidae			
Echinostomum sp.	*Nereis diversicolor, Nereis succinea*	Azov Sea	Latysheva 1939; Nechaeva 1964
"Echinostome"	*Nereis diversicolor*	Scotland	Burt 1962
Himasthla leptosomum[d]	*Arenicola marina*	English Channel, Bay of Biscay (France)	Caullery and Mesnil 1900; Cuénot 1912
Himasthla militaris[d]	*Nereis diversicolor, Arenicola marina*	Mediterranean (France), Baltic Sea	Timon-David and Rebecq 1958; Rebecq 1964; Reimer pers. commun.
Gymnophallidae			
Gymnophallus nereicola	*Nereis diversicolor*	Mediterranean (France)	Timon-David and Rebecq 1958; Rebecq and Prévot 1962; Rebecq 1964
Parvatrema borealis	*Nereis succinea, Nereis virens*[b]	Woods Hole, Mass. and San Francisco Bay (USA)	Stunkard 1962; Oglesby 1965
Undetermined family			
Cercaria parvicaudata	*Nereis virens*[b]	Woods Hole, Mass. (USA)	Stunkard 1950
Distoma myzostomatis	*Myzostomum platypus*	?	Wheeler 1896
Distomum sp.	*Nereis virens*	Atlantic coast, Canada	Stafford 1907
Unnamed metacercariae (3 types)	*Nereis succinea, Nephtys hombergi*	Azov Sea	Latysheva 1939
Unnamed metacercaria	*Onuphis conchylega*	Barents Sea	Amosova 1955
Unnamed progenetic metacercaria	*Nereis succinea*	Azov Sea	Latysheva 1939

[a]Due to inaccessibility of some early literature, a few records of unidentified metacercariae have been omitted.
[b]Infected experimentally, natural infections unknown.
[c]See text for comments on experimental hosts.
[d]Some authors regard *H. leptosomum* to be a synonym of *H. militaris*. Possibly all the echinostomatid records from polychaetes are referable to a single species.

Stunkard (1941) was unable to infect sea urchins, but readily infected *N. virens*, whereas with the closely related European *Zoogonus rubellus* the reverse was true. Further evidence of the specificity exhibited by *Z. lasius* is provided by the experimental work of Shaw (1933). She exposed a number of polychaetes (*N. virens*, *Hydroides* sp., *Lumbrineris hebes*, *Scoloplos robustus*, and *Arabella iricolor*) and the turbellarian *Bdelloura candida* to the cercariae (known originally as *Cercariaeum lintoni*) of this species. Full development to the metacercarial stage occurred only in *N. virens*. Although some cercariae penetrated and encysted in the other worms, they died within their cysts without reaching full development. These experiments suggest a physiological or immunological incompatability between the parasite and the tested hosts other than *N. virens*.[1]

Examples of species that are not limited to polychaetes in their choice of second intermediate hosts are *Opechona bacillaris* (coelenterates, chaetognath, mollusc), *Proctoeces maculatus* (molluscs), *Derogenes varicus* (chaetognath, crustaceans), *Asymphylodora demeli* (molluscs), and *Parvatrema borealis* (mollusc). An interesting situation occurs in *Lepocreadium setiferoides*. Martin (1938) was able to infect experimentally *Spio* sp. and a turbellarian, but not *Nereis* sp.

Most of the metacercariae occurring in polychaetes are encysted, but at least one species, *P. maculatus*, lies free in the coelom of its *Nereis* host, attached by its ventral sucker to the intestine or the body wall. Another exception is *G. nereicola*. Despite being histozoic, a cyst wall is not formed around each metacercaria. Rather, groups of metacercariae become enveloped in a mucous sac of irregular shape, representing a reaction of the host.

Although the location of the metacercariae within the body of the polychaete host has not always been mentioned, there are sufficient reports to establish that the location varies according to species of trematode. *Zoogonus lasius* and *G. nereicola* show a predilection for the parapodia; *Lepidapedon gadi* occurs in the body wall, especially at the base of the parapodia; *D. inflata* is found primarily in the body wall and the peribuccal region; *P. maculatus* and Mrázek's (1917) hemiurid occur in the coelom; and *Distoma myzostomatis* is located in the wall of the anterior part of the pharynx. *Himasthla militaris* and *P. borealis* show greater variation in their sites of encystment. The former occurs in the coelom attached to the body wall, in the body wall itself, or less frequently in the parapodia; the latter invades the ventral nerve cord, the nephridia, and the dorsal lobes of the parapodia.

Among the metacercariae found in polychaetes, perhaps *D. myzostomatis* deserves special mention since it represents a case of hyperparasitism, its host, *Myzostomum platypus*, being parasitic in the crinoid *Actinometra nobilis*. From one to five specimens of *D. myzostomatis* were found in each of eight *M. platypus* studied by Wheeler (1896). The adult of this trematode is unknown, nor is it known if *M. platypus* is its only second intermediate host.

Cestoidea

The cestodes of aquatic vertebrates all undergo part or all of their larval development in invertebrates. Larvae of a few species have been reported from polychaetes.

Cysticercoid larvae of the cyclophyllidean cestode *Ophryocotyle proteus* have been found in *Nereis diversicolor* from the mud flats of the River Eden, Scotland (Burt 1962). The cysticercoids occurred in the coelom of the posterior region of the polychaete, attached to the outer wall of the intestine. This tapeworm has a two-host life cycle, its definitive hosts being mainly certain wading birds.

Other larval cestodes from polychaetes have not been specifically or even generically identified. There are at least two records of the order Trypanorhyncha, the adults of which parasitize elasmobranchs. According to Dollfus (1923), as early as 1684 F. Redi reported a trypanorhynchan larva from *Aphrodita aculeata*. Redi called it "Vermi dell'Istrice marino." Later authors referred to Redi's specimen under a variety of names (*Vermis aphroditae aculeatae*, *Vermes histrycis marinae*, *Tetrabothriorhynchus aphrodite*, and *Tetrarhynchus aphroditae*), but the species has not been observed since its original account. Caullery and Mesnil (1900) note that A. de Saint-Joseph, in 1894, reported finding a *Tetrarhynchus* larva in the intestine of *Polycirrus denticulatus*.

Finally, the tapeworms provide another example of hyperparasitism. Wheeler (1896) cites Nansen (1885) as giving a brief account of a "tape-worm *Cysticercus*" from the alimentary tract of *Myzostomum graffi*. Nansen named the parasite *Taenia myzostoma*. Nothing is known of its adult stage and definitive host, but it is surely not a member of the genus *Taenia* as recognized now.

[1]Glading (1935) experimentally infected *Capitella* sp., *Eteone* sp., *Streblospio* sp., and *Nereis* sp. with *Cercariaeum lintoni*. From his results it is not possible to determine if the cercariae developed into infective metacercariae in all these polychaetes. See Stunkard (1938) for remarks on Glading's experiments.

It is noteworthy that the larvae of cestodes (Pseudophyllidea) parasitizing marine teleosts have not as yet been reported from polychaetes.

Nematoda

Among the nematodes of vertebrates, two genera, representing two superfamilies or orders, have been reported to use polychaetes as intermediate hosts.

Recent studies (Shulman and Shulman-Albova 1953; Popova et al. 1964; Popova and Valter 1965, 1967; Valter 1970) have established that *Antinoella sarsi*, *Eunoe nodosa*, *Gattyana cirrosa*, *Harmothoe imbricata*, *Lepidonotus squamatus*, and *Nereis pelagica* in the White Sea are natural hosts of larvae of *Contracaecum* (or *Thynnascaris*) *aduncum*, a common parasite of teleosts. In single infections, which constitute the majority of cases, the larvae usually occur free in the coelom in the vicinity of the pharynx and rarely in the middle part of the body. In multiple infections a greater portion of the coelom is occupied by the parasites, and in massive infections (54–170 larvae) of *E. nodosa* the larvae also invade the gonads and the muscle layer of the body wall; in this host many larvae become encapsulated.

Although other invertebrates (amphipods, copepods, chaetognaths) also serve as intermediate hosts of *C. aduncum*, the incidence of infection in *L. squamatus* and *H. imbricata* (16.6% and apparently 7–7.5%, respectively, according to data in Popova and Valter 1967) indicates that these annelids are probably important intermediate hosts, at least in the White Sea.

L. W. Reimer (personal communication) found *Contracaecum* larvae (probably *C. aduncum*) in the pelagic polychaete *Tomopterus helgolandica* in the Baltic Sea. The earlier records of McIntosh (1900) and Schultz (1911) of *Ascaris* larvae in the peri-pharyngeal space of *Harmothoe imbricata* from Great Britain and the Baltic, respectively, probably also are referable to *C. aduncum*.

The only parasites of mammals that have been reported to use polychaetes as intermediate hosts are nematodes of the genus *Parafilaroides*, which live in the lungs of pinnipeds. Mozgovoy, Popova, and Shakhmatova (in Skrjabin et al. 1963 p. 150) experimentally infected *Nereis pelagica* with larvae of *Parafilaroides gymnurus* obtained from the ringed seal *Pusa hispida*. The larvae settled unencysted in the coelom of the polychaete. Kurochkin (1964) subsequently reported finding larval nematodes he considered as probably *Parafilaroides caspicus* in the body cavity of *Nereis diversicolor* from the Caspian Sea. The definitive host of this lungworm is the Caspian seal (*Pusa caspica*), which, according to Kurochkin, feeds frequently on *Nereis*. Whether the larvae found in *Nereis* are infective for seals remains to be determined. The Soviet authors consider *P. gymnurus* and *P. caspicus* to have two-host life cycles, with *Nereis* species being the intermediate host. However, *Nereis* species are not native to the Caspian Sea, *N. diversicolor* having been first introduced there from the Azov Sea in 1939 (Karpevich 1968). Assuming that *Parafilaroides caspicus* is indigenous to the Caspian Sea, there must have been another intermediate host prior to the introduction of *Nereis*. Of interest in this connection is Dailey's (1970) recent elucidation of the life cycle of another species of *Parafilaroides*, *P. decorus*, from the California sea lion, *Zalophus californiensis*. In this species, a two-host life cycle was demonstrated experimentally, but the intermediate host is a fish.

Discussion

Of the four major groups of endoparasitic helminths of vertebrates, Trematoda (Digenea), Cestoidea, and Nematoda have species that use polychaetes as intermediate hosts in the course of their life cycle. Only the Acanthocephala, apparently, are not known to have enlisted the services of polychaetes for larval development. By comparison with the other helminth groups, the Trematoda have been the greatest exploiters of polychaetes.

In surveying the array of polychaetes that have been implicated as intermediate hosts (Table 2), no particular group stands out as unique in this respect, except perhaps the tube-dwelling Polychaeta Sedentaria as first intermediate hosts of digenetic trematodes. Even parasitic polychaetes (Myzostomidae) have been reported as hosts of larval helminths.

Since polychaetes are mainly benthic creatures, the majority of intermediate host records are to be found among the benthic species. However, pelagic polychaetes such as the Tomopteridae also serve as intermediate hosts for some helminths. In view of Carrère's unpublished observations (see Rebecq 1964) that *Nereis* (i.e. *Platynereis*) *dumerili* becomes infected with the trematode *Deropristis inflata* during pelagic stages or periods in its life, one cannot assume benthic species are necessarily infected in the that benthic environment. However, infection in the pelagic zone would only be possible with helminths having larvae that are capable of swimming or are free-floating. In the case of *D. inflata*, the cercariae are of the trichocercous type and hence capable of swimming. In contrast, the cercariae of *Zoogonus lasius* and *Zoogonoides laevis* lack tails and are not able to swim; nor are they free-floating. For contact

TABLE 2. List of polychaetes and their larval helminth parasites.[a]

POLYCHAETA ERRANTIA

Alciopidae — *Alciope* sp.
Lepocreadium album metacercaria (Trematoda)
Aphroditidae — *Aphrodita aculeata*
Larval trypanorhynch (Cestoidea)
Nephtyidae — *Nephtys hombergi*
Unidentified metacercariae (Trematoda)
Nereidae — *Nereis* (*Neanthes*) *caudata*
Proctoeces maculatus metacercaria (Trematoda)
— *Nereis* (*Neanthes*) *diversicolor*
Asymphylodora demeli metacercaria (Trematoda)
Deropristis inflata metacercaria (Trematoda)
Echinostomum sp. metacercaria (Trematoda)
"Echinostome" metacercaria (Trematoda)
Gymnophallus nereicola metacercaria (Trematoda)
Himasthla militaris metacercaria (Trematoda)
Ophryocotyle proteus cysticercoid (Cestoidea)
Parafilaroides caspicus (Nematoda)
— *Nereis* (*Neanthes*) *succinea*
Echinostomum sp. metacercaria (Trematoda)
Parvatrema borealis metacercaria (Trematoda)
Unidentified metacercariae (Trematoda)
— *Nereis* (*Neanthes*)*virens*
Cercaria parvicaudata metacercaria (Trematoda)
Deropristis inflata metacercaria (Trematoda)
Parvatrema borealis metacercaria (Trematoda)
Zoogonoides laevis metacercaria (Trematoda)
Zoogonus lasius metacercaria (Trematoda)
Unidentified metacercaria (Trematoda)
— *Nereis* (*Nereis*) *pelagica*
Lepidapedon gadi metacercaria (Trematoda)
Contracaecum aduncum (Nematoda)
Parafilaroides gymnurus (Nematoda)
— *Platynereis dumerili*
Deropristis inflata metacercaria (Trematoda)
Onuphidae — *Onuphis* (*Nothria*) *conchylega*
Unidentified metacercariae (Trematoda)
Polynoidae — *Antinoella sarsi*
Contracaecum aduncum (Nematoda)
— *Eunoe nodosa*
Contracaecum aduncum (Nematoda)
— *Gattyana cirrosa*
Contracaecum aduncum (Nematoda)
— *Harmothoe imbricata*
Derogenes varicus metacercaria (Trematoda)
Lepidapedon gadi metacercaria (Trematoda)
Ascaris sp.
Ascaris specialis (Nematoda)
Contracaecum aduncum (Nematoda)
— *Lepidonotus squamatus*
Lepidapedon gadi metacercaria (Trematoda)
Contracaecum aduncum (Nematoda)
Tomopteridae — *Tomopterus helgolandica*
Didymozoidae metacercaria (Trematoda)
Opechona bacillaris metacercaria (Trematoda)
Contracaecum sp. (Nematoda)
— *Tomopterus vitrina* (? = *T. helgolandica*)
Hemiuridae metacercaria (Trematoda)

POLYCHAETA SEDENTARIA

Ampharetidae — *Amphicteis gunneri floridus*
Cercaria amphicteis redia and cercaria (Trematoda)
Arenicolidae — *Arenicola marina*
Himasthla leptosoma metacercaria (Trematoda)
Himasthla militaris metacercaria (Trematoda)
Cirratulidae — *Cirriformia tentaculata*
Unidentified encysted nematode
Serpulidae — *Hydroides* (*Eupomatus*) *dianthus*
Cercaria loossi sporocyst and cercaria (Trematoda)
— *Hydroides norvegica*
Proctoeces maculatus metacercaria (Trematoda)
Spionidae — *Spio* sp.
Lepocreadium setiferoides metacercaria (Trematoda)
Terebellidae — *Alkmaria romijni*
Asymphylodora demeli metacercaria (Trematoda)
— *Lanicides vayssierei*
Cercaria hartmanae redia and cercaria (Trematoda)
— *Polycirrus denticulatus*
Tetrarhynchus sp. (Cestoidea)

MYZOSTOMIDA

Myzostomidae — *Myzostomum graffi*
"*Taenia*" *myzostoma* cysticercus (Cestoidea)
— *Myzostomum platypus*
Distoma myzostomatis metacercaria (Trematoda)

UNIDENTIFIED POLYCHAETES

Homalometron pallidum metacercaria (Trematoda)

[a]Hartman (1959, 1965) was followed for polychaete nomenclature, except that *Neanthes*, *Nothria*, and *Eupomatus* are regarded as subgenera rather than genera.

with their polychaete host, *Nereis virens*, they depend on being deposited by their molluscan host near the prospective polychaete host and being drawn into the latter's burrows by water currents (Stunkard 1938).

With the probable exception of the three species of trematode cercariae produced in tubiculous polychaetes, infection of the definitive host is through ingestion of polychaetes infected with larval stages of the parasites. Fishes are probably the most important predators of polychaetes; hence, it is not surprising that in the evolution of life-history patterns of helminth parasites of vertebrates, those in fishes have made greatest use of polychaetes as intermediate hosts.

As polychaetes are looked at more closely by parasitologists, undoubtedly the list of larval helminth–polychaete associations will expand. Apart from simply adding to the records, much remains to be learned about the ecology of larval helminth parasitism of polychaetes and the effects these parasites have on the behaviour, physiology, and survival of their polychaete intermediate hosts.

Acknowledgments

The stimulus to write this paper came from the author's association with the Berkeleys and the desire to participate in the tribute being paid to them with the publication of the present issue.

The Berkeleys are responsible for my first encounter with helminth parasites of polychaetes. In 1953, not long after my arrival at the Biological Station, they presented me with photographs of a metacercaria and a nematode taken by W. L. Klawe from *Eteone longa* at Wedgeport, N. S. Perhaps this is only of historical interest, because the photographs do not show sufficient detail to permit identification of the parasites, but they aroused my interest in the role of polychaetes in transmitting helminths to vertebrates.

Dr R. Ph. Dollfus (Muséum Nationale d'Histoire Naturelle, Paris) kindly allowed me the use of his documentation on nematode parasites of polychaetes, for which I am very grateful. I also thank Prof L. W. Reimer (Pädagogisches Institut, Güstrow, DDR) for providing me with unpublished information on polychaetes as intermediate hosts of helminths in the Baltic Sea.

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Descriptions of *Sthenelais fusca* Johnson 1897 and *S. berkeleyi* n.sp. (Polychaeta: Sigalionidae) from the Eastern Pacific

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PETTIBONE, M. H. 1971. Descriptions of *Sthenelais fusca* Johnson 1897 and *S. berkeleyi* n.sp. (Polychaeta: Sigalionidae) from the eastern Pacific. J. Fish. Res. Bd. Canada 28: 1393–1401.

Two sigalionid polychaete species were found to have been confused under *Sthenelais fusca* Johnson. The second species is named *S. berkeleyi* in honor of Dr Cyril Berkeley.

PETTIBONE, M. H. 1971. Descriptions of *Sthenelais fusca* Johnson 1897 and *S. berkeleyi* n.sp. (Polychaeta: Sigalionidae) from the eastern Pacific. J. Fish. Res. Bd. Canada 28: 1393–1401.

Deux espèces de polychètes sigalionides avaient été confondues et décrites sous le nom de *Sthenelais fusca* Johnson. Le nom de *S. berkeleyi* est donné à la seconde espèce en l'honneur de M. Cyril Berkeley.

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IN connection with a long range revision of the polychaete worms of the superfamily Aphroditoidea, including the Sigalionidae, it became apparent that two species had been confused under *Sthenelais fusca*. Johnson (1897) described *S. fusca* from four specimens found at low water in crevices under stones and among roots of *Phyllospadix* in the vicinity of Los Angeles (San Pedro) and San Francisco (Pillar Point, San Mateo County, and Bolinas, Marin County), California. The measurements for a full-grown specimen of about 140 segments was given as 95 mm in length and 7 mm in width. Later, Johnson (1901) identified as *S. fusca* a single anterior fragment of huge dimensions, 107 mm in length for 74 segments and a width of 12 mm, from Pleasant Beach, Seattle, Washington. Pettibone (1953) gave a more complete description of some large Puget Sound specimens under *S. fusca*. Johnson's material apparently no longer exists, but additional sigalionids, agreeing with Johnson's original description, and collected near the type-localities, were available for study in the Smithsonian Institution (USNM) and the Allan Hancock Foundation (AHF). A specimen from Naden Harbor, Queen Charlotte Islands, reported by Berkeley and Berkeley (1962) as *S. articulata* Kinberg, proved to belong rather to the Puget Sound species.

I take pleasure in naming this Puget Sound species *S. berkeleyi* in honor of Dr Cyril Berkeley, who, with his wife Edith, carried out pioneer studies on the polychaetes. Their publications still serve as the primary source for information on the polychaetes of western Canada and nearby areas. Their collections, now deposited in the Smithsonian Institution (Pettibone 1967), have been and are continuing to be utilized by other polychaete workers for checking and revisionary studies. Since my 1967 paper, in which the polychaete publications of Edith and Cyril Berkeley were listed, three additional papers have been published by Cyril Berkeley (1966, 1967, 1968). I count it a great privilege to have known both Cyril and Edith Berkeley through personal contacts, through their friendly and helpful correspondence, as well as through their scholarly publications.

Abbreviations Used in Figures

I–IV, segments; *acL*, acicular lobe; *au*, auricle; *a-vB*, anteroventral bract; *b*K, basal knob; *br*, branchia; *buC*, buccal cirrus; *ct*, ctenidia; *dR*, dorsal ridge; *dTc*, dorsal tentacular cirrus; *dTu*, dorsal tubercle; *IpaS*, inner palpal sheath; *ItL*, inner tentacular lobe; *lAn*, lateral antenna; *mAn*, median antenna; *nuO*, nuchal organ; *pa*, palp; *pB*, posterior bract; *st*, stylode; *vC*, ventral cirrus; *vTc*, ventral tentacular cirrus.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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Sthenelais Kinberg 1855

Both *S. fusca* Johnson and *S. berkeleyi* n.sp. show the following generic characters: Body elongate, vermiform, with numerous segments; middorsal ridge on some anterior segments, bordered by few pairs of small ctenidia. Elytra numerous pairs, on segments 2, 4, 5, 7, alternate segments to 27, and continuing on all segments. Elytra large, covering dorsum, with microtubercles and lateral fringes of papillae. Dorsal tubercles on segments 3, 6, 8, and alternate segments to 26. Prostomium rounded, fused to first or tentacular segment; median antenna with stout cylindrical ceratophore furnished with lateral auricles and terminal style; lateral antennae fused to inner dorsal sides of tentacular parapodia; four eyes; palps emerging ventral to tentacular parapodia; paired oval nuchal organs. Tentacular parapodia extending anteroventrally to prostomium, each with pair of tentacular cirri, single aciculum, two bundles of capillary setae, L-shaped inner tentacular lobe with ciliated ridge and fused to inner palpal sheath; ciliated dorsal ctenidium. Parapodia of second or buccal segment extending anteriorly, with ventral buccal cirri longer than those following; small ctenidia on lateral lips and medial to ventral cirri on some anterior segments. Third segment with dorsal tubercles fused to posterior sides of elytrophores of segment II. Neurosetae of segments II and III compound falcigerous with articulated blades and bifid tips.

Branchiae cirriform, ciliated, on external borders of all elytrophores and dorsal tubercles except for few anterior ones. Parapodial ctenidia cup-shaped, ciliated, three per parapodium, beginning on segment II. Parapodia with accessory bracts and stylodes. Notopodia clavate, with bracts nearly encircling acicular lobes. Notosetae numerous, arranged in semicircular row and directed posterodorsally, finely spinous, and tapering to capillary tips. Neuropodia with conical acicular lobes; bilobed C-shaped posterior bracts directed anteriorly on upper and lower margins; crescent-shaped anteroventral and anterior upper bracts. Neurosetae arranged in three groups: upper group within anterior upper bracts, C-shaped group of stouter neurosetae within posterior bracts, and lower arched group of more slender neurosetae within anteroventral bracts. Neurosetae simple spinous (in upper group) and compound falcigerous with some blades articulated and tips bifid; distal parts of stems smooth or spinous. Ventral cirri subulate, with outer basal knobs. Pharynx with 11 pairs of papillae and two pairs of jaws.

Sthenelais fusca Johnson

Fig. 1–3

Sthenelais fusca Johnson 1897 p. 185, p. 19: fig 60, 61, 61a, b; pl. 10: fig. 64, 64a–g. Monro 1933 p. 16. Berkeley and Berkeley 1935 p. 767; 1941 p. 26. MacGinitie 1935 p. 690. Hartman 1939 p. 61, pl. 13: fig. 153–162 (part; not fig. 160).

Not *Sthenelais fusca* Johnson 1901 p. 397. Pettibone 1953 p. 73. (=*S. berkeleyi* n.sp.).

Sthenelais variabilis var. *colorata* Monro 1933 p. 14, fig. 7. Not Monro 1924.

Material examined — *Central California*: Dillon Beach, May 28, 1941, under rocks, M. Pettibone collector, 1 specimen (new record; USNM 32386). *Southern California*: Elkhorn Slough, Monterey Bay, G. E. MacGinitie collector, 1 specimen (USNM 35024). San Pedro, Los Angeles, June 14, 1950, W. E. B. collector, 1 specimen (AHF). *Ecuador*: Salinas, September 12, 1926, W. L. Schmitt collector, 1 specimen (new record; USNM 24175). *Peru*: Paita, October 8, 1926, W. L. Schmitt collector, 1 specimen (new record; USNM 24173).

Description — Length up to 130 mm, width 5–7 mm, including setae, segments numerous (about 200). Wide middorsal ridge on segments 2–6, with 3–4 pairs of small ctenidia alongside (Fig. 1*a*). Ventral surface smooth, not papillate. Elytra suborbicular, subrectangular to subreniform, rusty brown, mottled with dark pigment, and sometimes with darker crescent-shaped areas medial to elytrophores. Elytra with uniformly distributed microtubercles except for lateral bare areas and some anterior bare areas in more posterior elytra; microtubercles low, rounded to slightly larger, subconical. Lateral borders with row of papillae and about 3 (3–6) irregular submarginal rows (Fig. 3*a*, *b*).

Prostomium with large lateral auricles on ceratophore of median antennae, ciliated on ventral side, and moderately long tapered style; lateral antennae short, subulate; 4 eyes arranged in square, moderate in size, anterior pair larger than posterior pair, partly concealed by auricles; palps extending to about segment 8 (7–10); nuchal organs large, partly hidden by first pair of cetnidia along middorsal ridge (Fig. 1*a*). Tentacular parapodia with dorsal tentacular cirrus subequal to median antenna; ventral tentacular cirri about half as long as dorsal cirri; inner tentacular lobe about same length as ventral tentacular cirrus, fused to shorter, rounded inner palpal sheath; dorsal ctenidium elongate-oval (Fig. 1*a*).

Parapodia of segments II and III directed anteriorly, slightly modified from following segments, with pair of small ctenidia on lateral lips (Fig. 1*a–d*). Blades of compound falcigerous neurosetae with 3–10 articles, with bifid tips; upper ones more slender, their tips sometimes appearing nearly entire; stems with numerous spinous rows (7–20); upper and lower neurosetae more slender than middle ones (Fig. 1*c*). Additional small ctenidia located medial to elytrophores of segment II and medial to ventral cirri of segments 3–7 (3–13 on specimen from Ecuador) (Fig. 1*a*, *d*).

Parapodia of anterior (Fig. 2*a*, *b*) and middle regions similar. Cirriform branchiae beginning on segment IV. Notopodial bracts fimbriated, lower anterior papillae or stylodes longer than dorsoposterior ones. Neuropodial acicular lobes without stylodes (except in more anterior parapodia). Upper lobes of bilobed posterior bracts with several stylodes on upper anterior part, lower lobes without stylodes. Anterior upper bracts indistinct, anteroventral bracts low, not fimbriated. C-shaped group of stout neurosetae with blades short to slightly longer, with stems smooth (Fig. 2*e*, *g*). Upper anterior group of neurosetae simple spinous (Fig. 2*c*) and compound falcigerous with blades of 3–5 articles

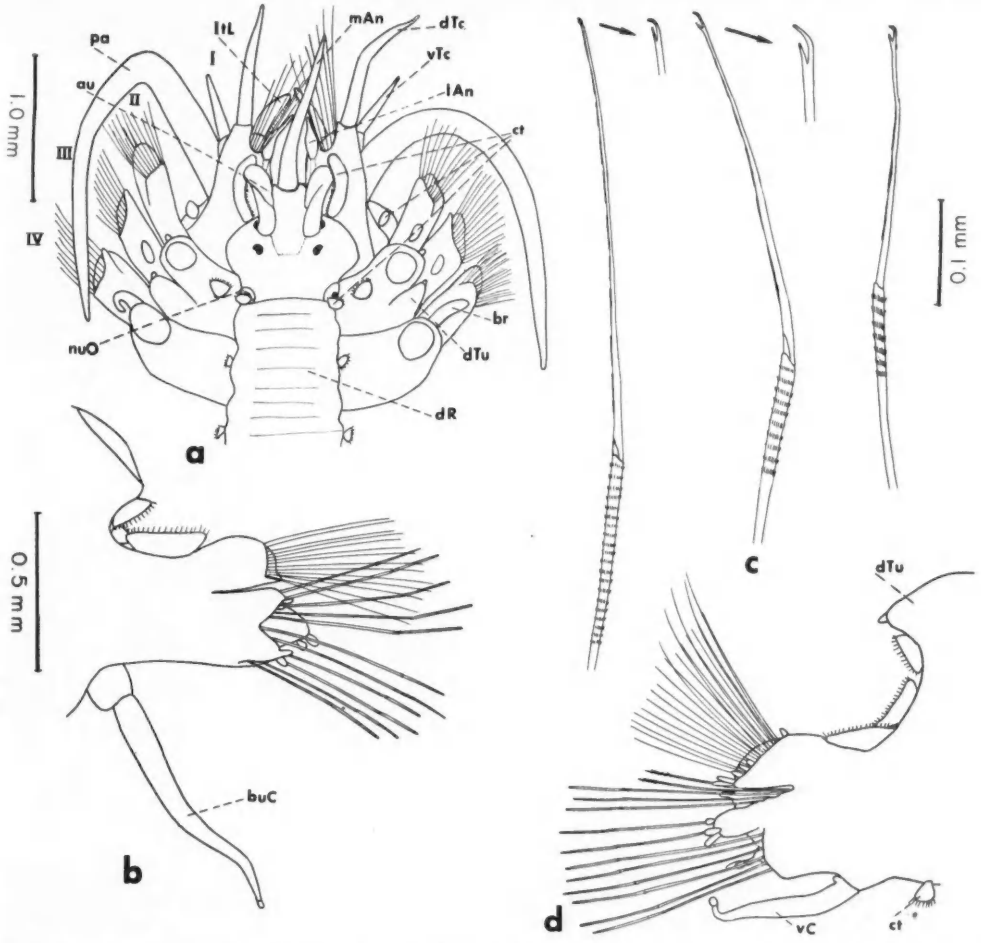

FIG. 1. *Sthenelais fusca* (USNM 35024): *a*, anterior end, dorsal view; *b*, second parapodium, posterior view; *c*, upper, middle, and lower neurosetae from same; *d*, third parapodium, anterior view.

and stems with 4–6 spinous rows (Fig. 2*d*). Anteroventral slender neurosetae with blades of 1–4 articles and stems with 3–5 spinous rows (Fig. 2*f*). Ventral cirri with distinct basal knobs.

Distribution — Central California to Peru. Low water.

Sthenelais berkeleyi n.sp.

Fig. 4–7

Sthenelais fusca Johnson 1901 p. 397. Pettibone 1953 p. 73, pl. 36: fig. 325–332; pl. 37: fig. 333–343. Not Johnson 1897.

Sthenelais tertiaglabra — Berkeley and Berkeley 1941 p. 26 (part). Not Moore 1910.

Sthenelais articulata — Berkeley and Berkeley 1962 p. 571. Not Kinberg 1855.

Material examined — *British Columbia*: Naden Harbor, Queen Charlotte Islands, 13 m, July 4–10, 1960, D. Quayle collector, 1 specimen (USNM 35029). *Washington, Puget Sound*: Shilshole Bay, south of entrance to Ballard Canal, tidal mud flat near low tide line, August 1934, J. E. Lynch collector, holotype (USNM 32365). South side of Salmon Bay near Government Locks, Ballard, mud and shingle exposed at low tide, May 11, 1937, J. E. Lynch collector, 2 paratypes (USNM 25457).

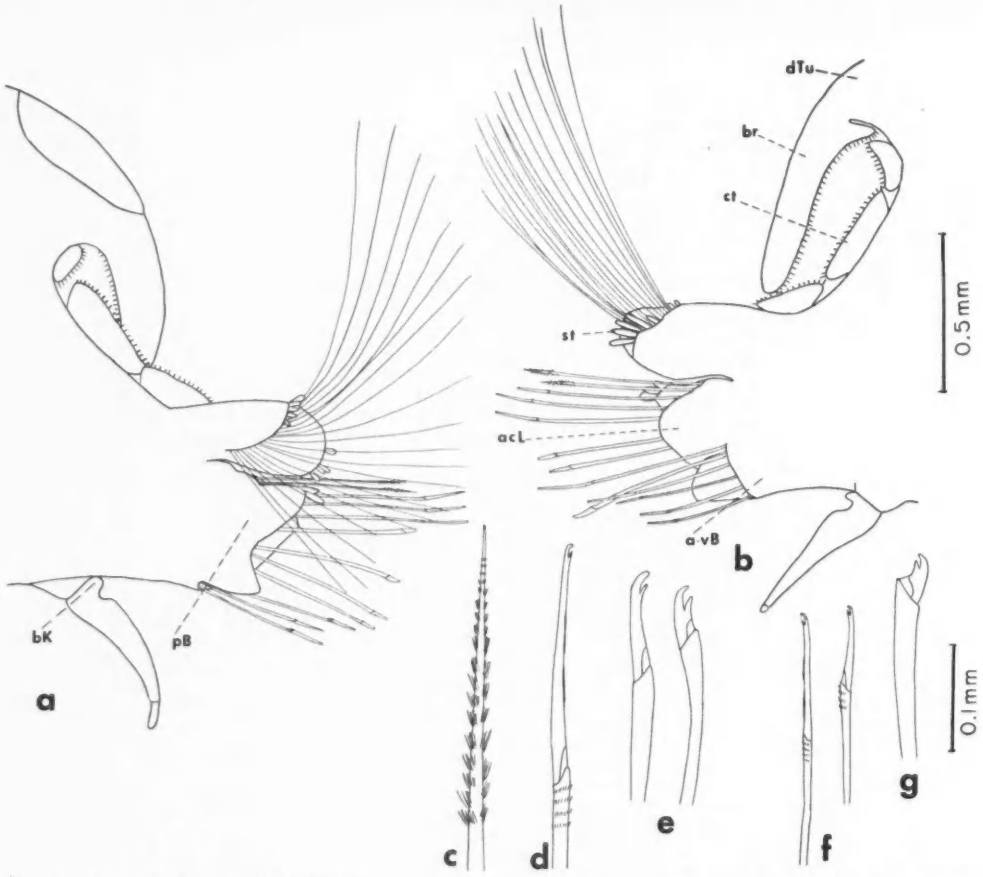

FIG. 2. *Sthenelais fusca* (USNM 35024): *a*, parapodium from anterior region, posterior view; *b*, same, anterior view; *c*, simple neuroseta; *d*, compound falcigerous neuroseta from upper anterior group; *e*, same, from middle group; *f*, same, from anterior ventral group; *g*, same, from middle group of parapodium from middle region.

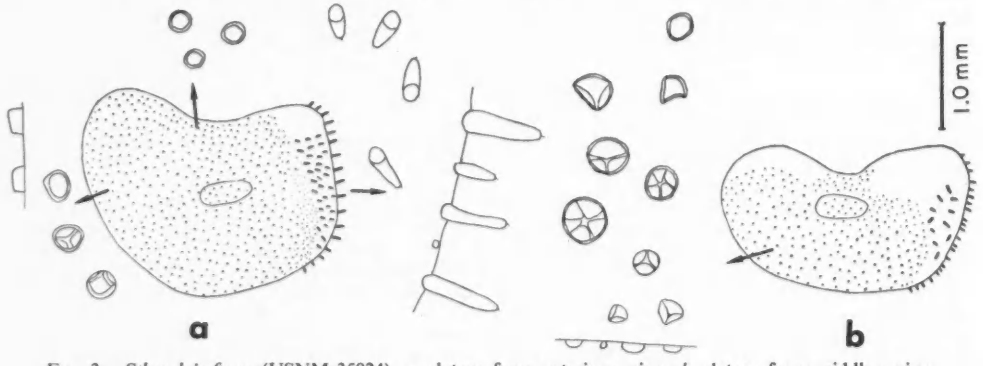

FIG. 3. *Sthenelais fusca* (USNM 35024): *a*, elytron from anterior region; *b*, elytron from middle region.

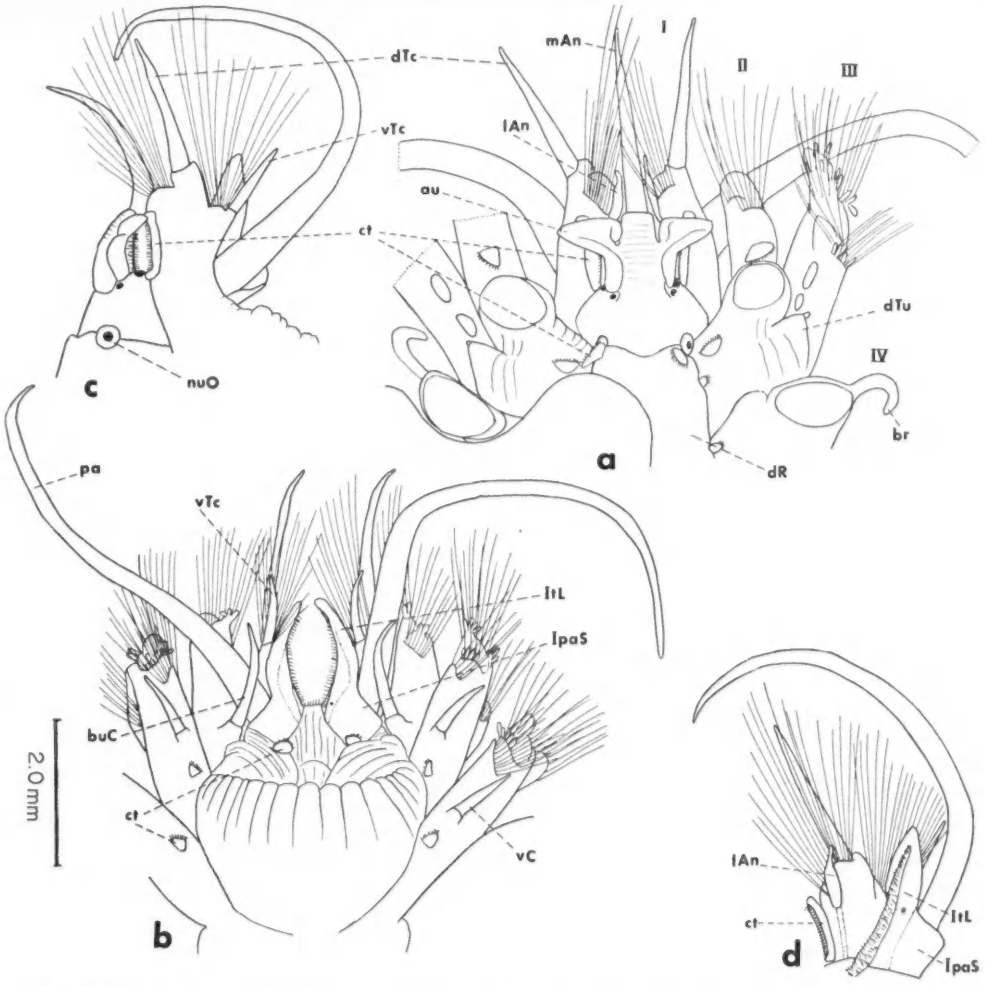

FIG. 4. *Sthenelais berkeleyi* n.sp. (paratypes, USNM 25457): *a*, anterior end, dorsal view; *b*, anterior end, ventral view; *c*, right tentacular parapodium, outer or lateral view; *d*, left tentacular parapodium, inner or medial view.

Browns Point, Tacoma, low tide, July 1946, M. H. Pettibone collector, paratype (USNM 25461). End of Colvos Passage, 110 m, gravel, August 2, 1938, M. H. Pettibone collector, paratype (USNM 25458). Off Foulweather Bluff and Point No Point, Admiralty Inlet, 70 m, shelly mud, July 8, 1940, M. H. Pettibone collector, paratype (USNM 25460). Off Cutts Island, Case Inlet, 30 m, August 2, 1938, M. H. Pettibone collector, 1 specimen (USNM 25465). *Southern California*: Off Balboa, 22–60 m, November 25, 1932, G. E. MacGinitie collector, 1 specimen (mixed with *S. tertiaglabra*, USNM 44517).

Description — Length of complete holotype 400 mm, width 12 mm, including setae, segments about 270. Length of incomplete paratypes 90–250 mm, width 8–13 mm, including setae. Wide middorsal ridge on segments 2–7, with 4 pairs of small ctenidia alongside (Fig. 4*a*). Ventral surface thickly papillate, with close-set short papillae and extending on ventral sides of parapodia, beginning anteriorly on body (not on lower lip; Fig. 6*a*, *b*). Elytra suborbicular, subrectangular to subreniform, pale to rusty brown. Elytra with uniformly distributed microtubercles, except for lateral partially bare areas and some anterior bare areas on more posterior

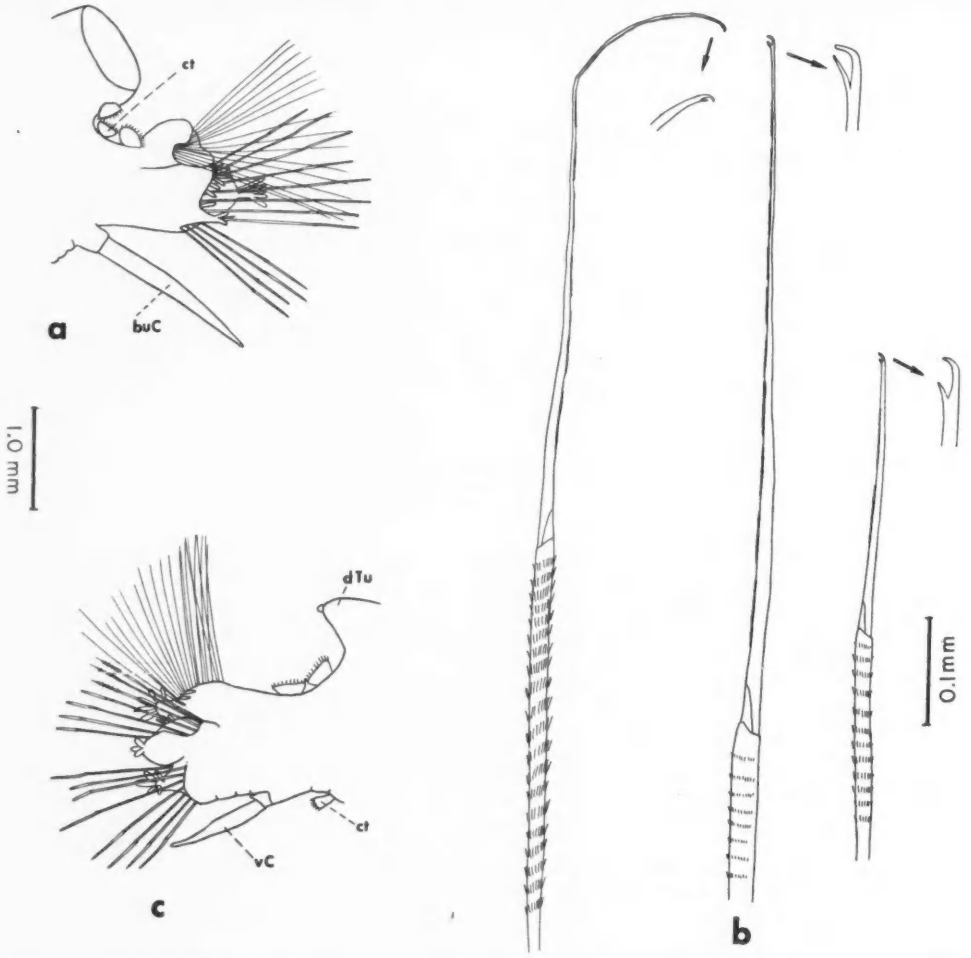

FIG. 5. *Sthenelais berkeleyi* n.sp. (paratypes, USNM 25457): *a*, second parapodium, posterior view; *b*, upper, middle, and lower neurosetae from same; *c*, third parapodium, anterior view.

elytra; microtubercles low, rounded to slightly larger, conical. Lateral borders of elytra with row of papillae, sometimes with additional minute sensory papillae, and few (4–7) irregular submarginal rows of papillae (Fig. 7*a*, *b*).

Prostomium with large lateral auricles on ceratophore of median antenna, ciliated on ventral side, and moderately long tapered style; lateral antennae short, subulate; 4 eyes in trapezoidal arrangement, moderate in size, anterior pair larger than posterior pair and partly concealed by auricles; palps extending to about segment 7–8; nuchal organs large, sometimes partly hidden by first pair of ctenidia along middorsal ridge (Fig. 4*a*).

Tentacular parapodium with dorsal tentacular cirrus subequal to median antenna; ventral tentacular cirri about half as long as dorsal cirrus; inner tentacular lobe about same length as ventral cirrus, fused to shorter, rounded inner palpal sheath; dorsal ctenidium elongate-oval (Fig. 4*a*–*d*).

Parapodia of segments II and III directed anteriorly, slightly modified from following segments (Fig. 4*a*, *b*; 5*a*–*c*). Blades of compound falcigerous neurosetae with 3–11 articles, with bifid tips; upper ones more slender, their tips sometimes appearing nearly entire; stems with numerous spinous rows (9–22); upper and lower neurosetae more slender than middle ones (Fig.

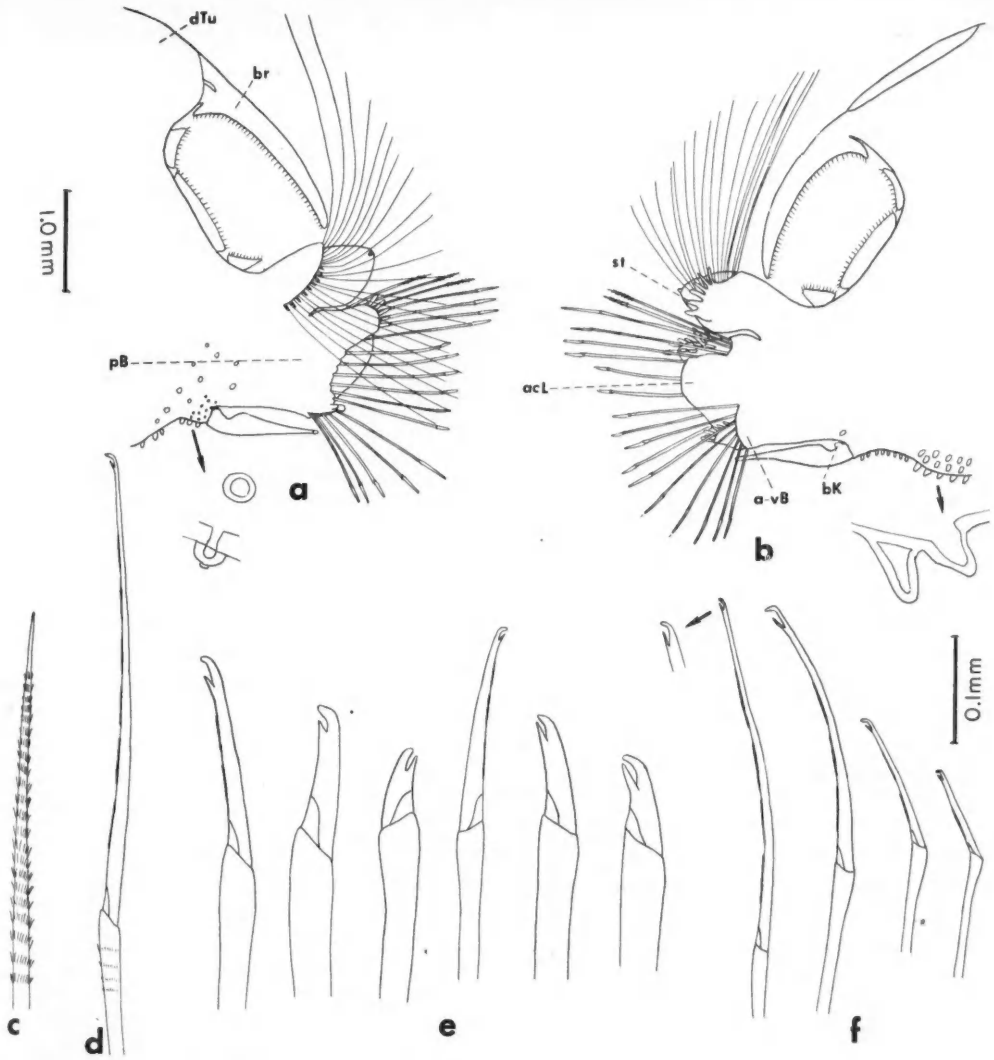

FIG. 6. *Sthenelais berkeleyi* n.sp. (paratypes, USNM 25457): *a*, parapodium from anterior region (about segment 25), posterior view; *b*, same, anterior view; *c*, upper simple neuroseta; *d*, compound falcigerous neuroseta from upper anterior group; *e*, same, from middle group; *f*, same, from anterior ventral group.

5*b*). Additional small ctenidia medial to elytrophores of segment II and medial to ventral cirri of segments 3–5 (Fig. 4*a*, *b*; 5*c*).

Parapodia of anterior (Fig. 6*a*, *b*) and middle regions similar. Cirriform branchiae beginning on segment IV. Notopodial bracts fimbriated, series of short papillae posteriorly and longer papillae on lower anterior part. Neuropodial acicular lobes without stylodes (except in more anterior parapodia). Bilobed posterior bracts with numerous stylodes on both upper and lower anterior parts. Anterior upper bracts indistinct, anteroventral bracts low, not fimbriated. C-shaped group of stout neurosetae with blades short to longer, formed of 1–4 articles, with stems smooth (Fig. 6*e*). Upper anterior

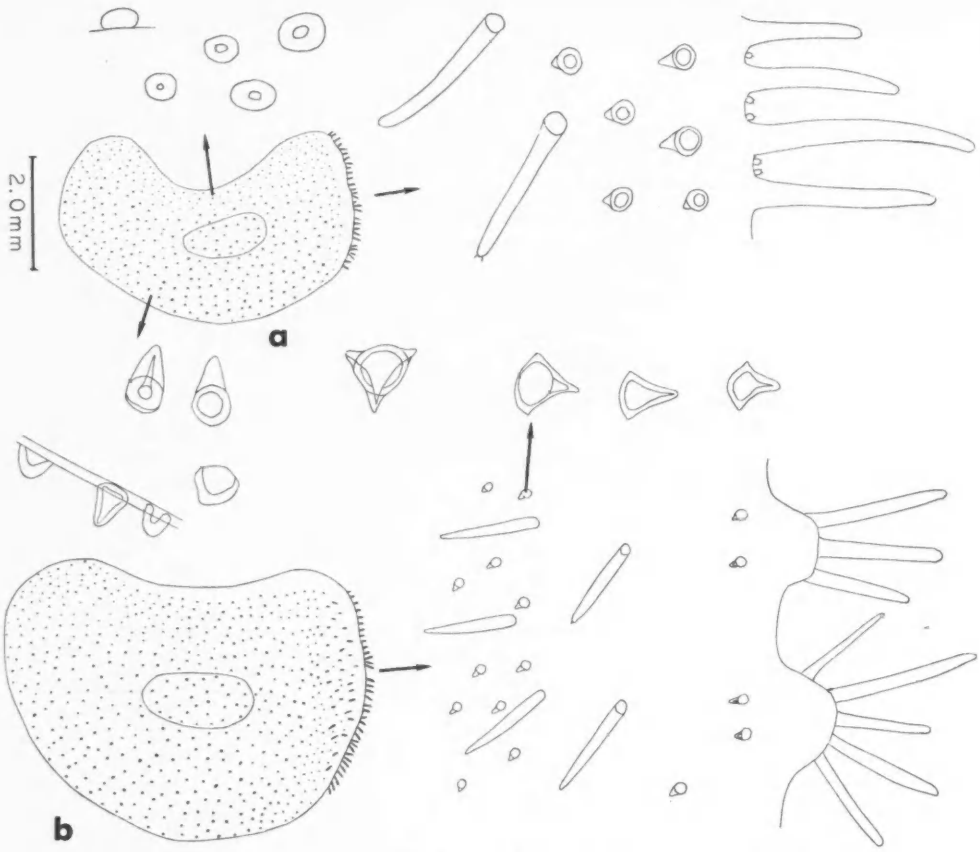

FIG. 7. *Sthenelais berkeleyi* n.sp. (paratypes, USNM 25457): *a*, third right elytron; *b*, 13th right elytron.

group of neurosetae simple spinous (Fig. 6*c*) and compound falcigerous with blades formed of about 7 articles and stems with about 4 spinous rows (Fig. 6*d*). Anteroventral slender neurosetae with blades of 1–4 articles and stems smooth (Fig. 6*f*). Ventral cirri with distinct basal knobs.

Distribution — British Columbia to Southern California. Low water to 110 m.

Remarks — *Sthenelais berkeleyi* may be distinguished from *S. fusca* by the following characters:

	S. fusca	*S. berkeleyi*
Ventral surface	Smooth, not papillate (Fig. 2*a*, *b*)	Thickly papillate (Fig. 6*a*, *b*)
Bilobed posterior bracts of neuropodia	Provided with few stylodes on upper anterior part; without stylodes on lower anterior part (Fig. 2*a*, *b*)	Provided with numerous stylodes on both upper and lower anterior parts (Fig. 6*a*, *b*)

Acknowledgments

This manuscript benefited from the suggestions of Dr F. M. Bayer of the University of Miami, Coral Gables, Florida.

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Amphipacific Distribution of Polychaetes

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USCHAKOV, P. V. 1971. Amphipacific distribution of polychaetes. J. Fish. Res. Bd. Canada 28: 1403–1406.

Some 25 polychaete species common to Asiatic and American coasts are recorded in south-boreal and subtropical waters of the Pacific; they are absent in both northern cold regions (Bering and Okhotsk seas) and in tropical zones. Examples are also given of analogous, closely related twin species, and subspecies. Such disjunct amphipacific ranges of these species are probably caused by ancient changes in climatic conditions. The possibility of modern oceanic currents having some influence on this is also not excluded. The author suggests a study of life cycles of amphipacific species in the extremes of their habitats.

USCHAKOV, P. V. 1971. Amphipacific distribution of polychaetes. J. Fish. Res. Bd. Canada 28: 1403–1406.

Quelque 25 espèces de polychètes communes aux côtes asiatique et américaine et réparties dans les eaux sud-boréales et semi-tropicales du Pacifique sont mentionnées; ces espèces sont absentes des régions nordiques (mers de Béring et d'Okhotsk) aussi bien que de la zone tropicale. L'auteur cite des exemples d'espèces et de sous-espèces jumelles étroitement apparentées. La répartition "amphipacifique" discontinue de ces espèces est sans doute le résultat de changements de vieille date des conditions climatiques. On n'exclut toutefois pas l'influence possible des courants marins actuels. L'auteur suggère l'étude du cycle vital d'espèces provenant des limites extrêmes de leurs habitats.

Received February 24, 1971

DURING the past 50 years numerous studies have been performed that make our knowledge of the polychaete composition and distribution in the North Pacific ocean considerably more precise. A substantial contribution was made by Edith and Cyril Berkeley, who published more than 50 works distinguished by an elaborate description of material. Owing to their work, we now have a better concept of the polychaete fauna of the British Columbia coast. According to their data, this comparatively small area of the Pacific contains about 365 species (Berkeley 1967, 1968). The Berkeleys' works are of great value, not only for the knowledge of polychaete fauna in Canadian waters, but also because they stimulated to some extent polychaete studies in all the North Pacific. In particular, they have been constantly used as references by Soviet scientists in their studies of Asiatic seas.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

Printed in Canada (J2060)

This article is an attempt to compare the polychaete shelf faunas of the Asiatic and American coasts of the North Pacific, which are influenced by different physical and geographical conditions, and to note some general zoogeographical problems.

Polychaete fauna of Japan was studied for a long time and described at length in two recently published volumes by Imajima and Hartman (1964). In the Soviet Union, polychaete studies in Far Eastern seas began in the 1920's. These were the works by Annenkova (1938) and Zachs (1933), which I continued and summarised in my book *Polychaeta of the Far Eastern Seas of the U.S.S.R.* (1955). This, however, is somewhat out of date now because there are many addenda and some emendations. Of more recent studies supplementing my work, those by Chlebovitsch (1961, 1962), Levenstein (1960, 1966), and Buzhinskaja (1967) should be mentioned. From 1957 to 1961, large collections of polychaetes were made in the Yellow and South China seas by joint Soviet–Chinese and Soviet–Vietnamese expeditions, resulting in a series of publications (Chlebovitsch and Wu 1962a, 1962b; Uschakov and Wu 1965; Wu 1962, 1964; Strelzov 1968; and many others).

Considering the previous studies, about 700 species are presently known from the different zoogeographical waters of the Northwest Pacific. Approximately 30% of the species of this fauna are considered endemic. A particular feature is that, in cold continental parts of the Bering and Okhotsk seas, where constant subzero temperatures prevail, many species the same as in the Arctic basin occur. I distinguish them as "arctic–far eastern" species (Uschakov 1955) and they accentuate a high specificity of the fauna of these seas. The sharpest change in faunal composition occurs at the southern Kurile Islands and Laperouse Strait. Some mingling of different zoogeographic elements can also be observed in the Yellow Sea, where, chiefly in deeper layers, several cold-water species occur, but upper layers are dominated by southern subtropical forms.

All data on polychaetes of the opposite side of the Pacific (coast of California) are summarized in two volumes of the Atlas by Hartman (1968, 1969); for this region more than 700 species are known.

In spite of differences in the faunas of the Asiatic and American shores of the North Pacific, forms common to the two areas do occur. Among the common forms that occur, those shelf species occurring both in south-boreal and subtropical waters on opposite coasts of the Pacific, but absent in the cooler northern parts, as well as in tropical zones, are of special interest. Such species with an interrupted distribution are called "amphipacific" (Andriashev 1939) and their disjunct range, "japano-oregonic." In his work Andriashev deals with the probable historic causes leading to the origin of such disjunct ranges in fishes and in several invertebrates. The problem was also touched upon by Gislén (1944), Ekman (1946), Djakonov (1955), and others. A study of polychaetes in Asiatic waters reveals many instances of amphipacific distribution. On the American coast, amphipacific species are distributed considerably farther north (up to the Gulf of Alaska) than on the coast of Asia. Some typical species are as follows:

Phyllodoce (*Anaitis*) *papillosa* Uschakov et Wu — Hainan Is., Yellow Sea, and ? California, USA (Hartman 1961 p. 63); *Eumida tubiformis* Moore — Yellow Sea, Sea of Japan, Kurile Is., and Vancouver Is.; *Eumida nigrimaculata* (Moore) — Sea of Japan, Kurile Is., Vancouver Is., and California; *Lepidasthenia interrupta* (Marenzeller) — Japan and California; *Glycera tenuis* Hartman — Yellow Sea, Oregon, and California; *Glycera robusta* Ehlers — Yellow Sea, Japan, and from Vancouver Is. to S. California; *Nicon moniloceras* (Hartman) — Yellow Sea, Hokkaido, California, and Mexico; *Nereis* (*Neanthes*) *neoneanthes* Hartman — Sea of Japan (Poseit Bay) and from Gulf of Alaska to Oregon; *Platynereis agassizi* (Ehlers) — Yellow Sea, Sea of Japan, South Sakhalin, southern Kurile Is., and from Gulf of Alaska to California; *Cheilonereis cyclurus* (Harrington) — Yellow Sea, Sea of Japan, Kurile Is., Hokkaido, Western Canada, and California; *Nephtys californiensis* Hartman — Yellow Sea, southern Kurile Is., Western Canada, and California; *Autolytus magnus* Berkeley — Hokkaido and Western Canada; *Trypanosyllis gemmipara* Johnson — Sea of Japan, Hokkaido, and Alaska south to Western Mexico; *Lumbrinereis cruzensis* Hartman — Yellow Sea, Vancouver Is., and California; *Dorvillea moniloceras* (Moore) — Yellow Sea, Sea of Japan, South Sakhalin, Western Canada, California, and Hawaiian Is.,; *Spiophanes berkeleyorum* Pettibone — Sea of Japan (Peter the Great Bay) and Western Canada; *Nerine alaskensis* (Treadwell) — southern Kurile Is. and Gulf of Alaska; *Polydora* (*Boccardia*) *uncata* Berkeley — Yellow Sea, Japan, and Western Canada; *Poecilochaetus johnsoni* Hartman — Yellow Sea and California; *Oncoscolex pacificus borealis* Imajima et Hartman — Sea of Japan (Peter the Great Bay), North Japan, southern Kurile Is., and Western Canada; *Isocirrus longiceps* (Moore) — Southern Kurile Is., Vancouver Is., and California; *Neoleprea californica* (Moore) — Sea of Japan, southern Kurile Is., and California; *Bispira polymorpha* Johnson — Sea of Japan, southern Kurile Is., and Alaska south to Western Canada; *Bispira vancouveri* (Kinberg) — Yellow Sea, Sea of Japan (Peter the Great Bay), southern Kurile Is., Western Canada, and California; *Fabricia pacifica* Berkeley — Yellow Sea and Vancouver Is.

In this list only species confined in their distribution to the North Pacific are included. There are also several amphipacific species having an amphiboreal distribution as well, such as *Nerine cirratulus* (Delle Chiaje), *Branchiomaldane vincenti* Langerhans, and others, but they are not considered here. The above list of polychaetes with amphipacific disjunct ranges is likely to be enlarged by further studies. *Halosydna nebulosa* Marenzeller from the coast of Japan and the Yellow Sea is probably an amphipacific species, because according to Imajima and Hartman (1964) it does not differ from *H. brevisetosa* Kinberg from the coast of California. There are also some other closely related twin species: *Dorvillea japonica* (Annenkova) — Sea of Japan, South Sakhalin, southern Kurile Islands, and *D. articulata* (Hartman) from California; *Schistocomus sovjeticus* Annenkova — Sea of Japan, Hokkaido, southern Kurile Islands; and *S. hiltoni* Chamberlin — Vancouver Is., Oregon, and California. Several closely related subspecies are described: *Rhynchospio arenicola asiatica* Chlebovitsch from Kurile Islands (typical form in California), and *Typosyllis aciculata orientalis* Imajima et Hartman from the coast of Hokkaido (typical form also in California).

Quite naturally, a thorough revision of closely related species is needed.

Unfortunately, there are no reliable paleontological remnants enabling us to elucidate the preceding stages of their distribution. One should agree with Andriashev's opinion that in preglacial time (i.e., Miocene and Pliocene), and also in interglacial periods of the Pleistocene, when the climate was considerably warmer, warmwater fauna was more widespread throughout the northern part of the Pacific, and mutual exchange of faunas between the two coasts was more intense than nowadays. But, in subsequent periods of sharp cooling, the majority of warmwater forms were driven out of northern parts of the Pacific and present disjunct ranges resulted. Besides these general historical events, which left a strong impression on all the fauna of the North Pacific, the possibility exists that amphipacific distribution of certain warmwater polychaete species resulted, to some extent, from transportation by oceanic currents. The mutual exchange of southboreal and subtropical forms between Asiatic and American shores of the North Pacific can be in progress at present also. Importance of currents for dispersal of marine invertebrates having pelagic larvae was shown by Thorson (1950). In polychaetes, the pelagic stage of development may occasionally be considerably prolonged (Monro 1931). From observations it is evident that polychaete larvae frequently spread over large expanses of the ocean (Mileikovsky 1968). Drifting seaweed (kelp) and floatage may be of essential assistance in their dispersal. Therefore, a thorough study of the role played by the Kuroshio (including the North Pacific current) and North Equatorial currents in polychaete dispersal is urgently needed. Then, I think, a comparative study, using standard methods, of the life cycles of some amphipacific species from their extreme habitats, would enable us to understand better the essence of disjunct distributions and the nature of adaptability in different polychaete species. This would provide abundant data for possible introductions, in order to raise the productivity in coastal regions. To solve such complicated problems, joint efforts of scientists of different countries engaged in studies of the North Pacific Ocean are essential.

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Abyssal Polychaetous Annelids from the Mozambique Basin off Southeast Africa, with a Compendium of Abyssal Polychaetous Annelids from World-Wide Areas[1]

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HARTMAN, O. 1971. Abyssal polychaetous annelids from the Mozambique Basin off southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. J. Fish. Res. Bd. Canada 28: 1407–1428.

Twenty-six abyssal polychaetes are named from the Mozambique basin off southeast Africa. Three species and two genera are new: ***Progoniada simplex***, ***Berkeleyia profunda***, ***Bruunilla natalensis***, and another in Sphaerodoridae to be described elsewhere. A new family Fauveliopsidae is erected, its species previously allied with Flabelligeridae. Three species are known from Indo-Pacific regions: *Glycera papillosa*, *Ammotrypane brevibranchiata*, *Phalacrostemma elegans*. One, *Axionice spinifera*, is antarctic; another, *Scalibregma inflata*, is cosmopolitan. Five generic categories are chiefly or wholly abyssal: *Ilyphagus*, *Fauveliopsis*, *Flabelligella*, *Monorchos*, *Potamethus*. Nine genera are cosmopolitan: *Aphrodita*, *Euphrosine*, *Phyllochaetopterus*, *Chaetozone*, *Ammotrypane*, *Nicomache*, *Myriochele*, *Serpula*. Unidentifiable species are in families Lacydonidae, Onuphidae, and Ampharetidae. A compendium names abyssal species from depths of 2000 m or more; included are nearly 500 species in 240 genera and 51 families.

HARTMAN, O. 1971. Abyssal polychaetous annelids from the Mozambique Basin off southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. J. Fish. Res. Bd. Canada 28: 1407–1428.

L'auteur énumère 26 polychètes abyssaux du bassin de Mozambique, au large de l'Afrique Sud-Orientale. Trois espèces et deux genres sont nouveaux: ***Progoniada simplex***, ***Berkeleyia profunda***, ***Bruunilla natalensis*** et un genre de Sphaerodoridae qui sera décrit ailleurs. On établit une nouvelle famille, celle des Fauveliopsidae, dont les espèces étaient auparavant alliées aux Flabelligeridae. Trois espèces sont connues dans les eaux indopacifiques: *Glycera papillosa*, *Ammotrypane brevibranchiata* et *Phalacrostemma elegans*. Une espèce, *Axionice spinifera*, est antarctique; une autre, *Scalibregma inflata*, est cosmopolite. Cinq groupes génériques sont surtout ou entièrement abyssaux: *Ilyphagus*, *Fauveliopsis*, *Flabelligella*, *Monorchos* et *Potamethus*. Neuf genres sont cosmopolites: *Aphrodita*, *Euphrosine*, *Phyllochaetopterus*, *Chaetozone*, *Ammotrypane*, *Nicomache*, *Myriochele* et *Serpula*. Il y a, au sein des familles des Lacydonidae, Onuphidae et Ampharetidae, des espèces non identifiables. Près de 500 espèces appartenant à 240 genres et 51 familles, et vivant à des profondeurs de 2000 m et plus sont énumérées en compendium.

Received February 25, 1971

THIS report embodies the study of the abyssal benthic biological samples taken off southeast Africa by the R/V *Anton Bruun*, in July–September 1964, of cruise 7 of the International Indian Ocean Expedition. The program was supported by the National Science Foundation, and the detailed studies by the Allan Hancock Foundation.

The greatest depths of the Mozambique basin are located in latitudes 23–36°S and longitudes 33–44°E, between the southeast coast of Africa and Madagascar. It comprises an area exceeding 30,000 square miles, and is separated from the more southern Antarctic basin by strong fracture zones. There is no previous knowledge of the kinds and numbers of benthic polychaetes from the Mozambique basin.

[1]The southern extension of Mozambique basin, in latitudes 23–27′S, continues southward to the Natal Basin, in latitudes 27–40′S.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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The Mozambique area was earlier (1950–52) sampled by the Danish *Galathea* under the direction of Dr A. F. Bruun. The sea bottoms off Durban and Natal, South Africa, from 440–2370 m, were found to be rocky, overlain by globigerina ooze and clay. The area off Natal, from 730–5020 m, is covered with globigerina ooze and sand, and the Mozambique channel, from 3220–3530 m, with globigerina ooze and clay (Bruun 1957 p. 34–36). Among 24 samples attempted by the *Galathea*, 15 were useless through lost, torn, or malfunctioning gear; only 5 yielded some results. This indicated the difficulties of sampling an area where topography, kinds of sediments, and current patterns are nearly unknown. Bruun described the currents of the Indian Ocean area: during all seasons a south equatorial current starting at Australia flows across the ocean south of the equator. Part turns south and follows the east African coast, where the most southerly continuation is called the Agulhas current. In the southernmost part of the ocean, a current starts south of Africa and goes eastward towards Australia.

Forty lowerings were attempted by the R/V *Anton Bruun*, using Campbell grab, trawls, and rock-dredge. Stations numbered from 361 to 388 (see station list) resulted in 26 samples that were useful to characterize the abyssal fauna. Ten samples from stations 361–371, from the northern end of the basin, contained no visible metazoan life. Fourteen others, from shallowest to greatest depths, contained some life. Compared with samples from shallower adjacent bottoms from the same general area, life is sparse to negligible and widely dispersed but equally diversified. In areas remote from shore, much of the bottom is covered by light brown clay, or globigerina ooze of unknown thickness, or with pteropod ooze in tropical latitudes. The southern end of the basin is strewn with black, globular, iron–manganese nodules measuring 2–20 cm across; some have a core of shark's-tooth or other biological remain.

The northern end of the basin is hard-surfaced, resulting from southerly flowing bottom currents. This was noted during sampling by a strong strain on the winch-line when lowered below 100-m depths; the current came from the north or northeast. Deep currents from the north are poor in kinds and numbers of settling larvae, or have adverse effects on benthic animals.

The samples yielded more than 100 species and about 200 specimens of metazoan invertebrate animals. Most species are represented by single or few specimens. Highest values were at station 360C, with 15 species and 18 specimens; station 388C had 14 species and 29 specimens; station 376D 11 species and 17 specimens; and station 361G 9 species and 21 specimens (see station list).

The best represented animal group was polychaetes, with 26 species; this was followed by small crustaceans, isopods, amphipods, tanaids, cumaceans, then small pelecypods, ophiuroids, and holothuroid echinoderms. A complete faunal list is given in the station list.

Systematic Account of the Polychaetous Annelids

APHRODITIDAE: *Aphrodita* sp., station 376D, a small juvenile, 4983 m.

EUPHROSINIDAE: *Euphrosine* sp., station 376D, a small juvenile, 4983 m.

LACYDONIIDAE: lacydonid, fragment, station 382C, 4886–5069 m.

SPHAERODORIDAE: unknown genus and species, station 376D (1), 4982 m.

GLYCERIDAE: *Glycera ?papillosa* Grube 1857, station 376D (1), 4983 m.

GONIADIDAE : *Progoniada simplex* n.sp.

Fig. 1

Record — Station 382C (3, type), 4886–5069 m.

Description — Body long and linear; 98 setigers measure 22.5 × 1.3 mm in the widest or pharyngeal region; a short posterior end lacking. Prostomium long, slightly depressed, and tapers to a truncate frontal margin with four biarticulated antennae; each has a short distal article. Eyes absent. First visible segment has a part of short broad cirri but no parapodia or setae. Next segment is first with parapodia and setae. Proboscis, seen by dissection, terminates distally in a circlet of soft papillae and dark jaws comprising a pair of black macrognaths with a large fang and several smaller teeth; dorsal arc of micrognaths has 3, and ventral arc 10 similar pieces; all unite to form a circlet. Proboscidial papillae of one kind, each a small mound with terminal pore (Fig. 1*a*). Paired chevrons (Fig. 1*a*) inconspicuous, near the pharyngeal base, and pale; each has 15 V-shaped pieces, in which the base is darkest.

Anterior parapodia have a short, triangular dorsal cirrus, a longer, more slender ventral cirrus, and a prolonged presetal lobe; acicular lobe short and distally rounded (Fig. 1*b*). Setae include 3 supra- and 3 subacicular composite spinigers, and a single, yellow, rodlike, embedded aciculum. Each of the spinigers has heterogomph articulation (Fig. 1*d*) and a long slender appendage with pointed tip and smooth cutting edge. Median and far posterior parapodia (Fig. 1*c*) resemble those in front but are larger; each has 2 or 3 superior, and 3 or 4 inferior composite spinigers and an embedded yellow aciculum.

Remarks — *Progoniada simplex* differs from *P. regularis* Hartman 1965, the only other named

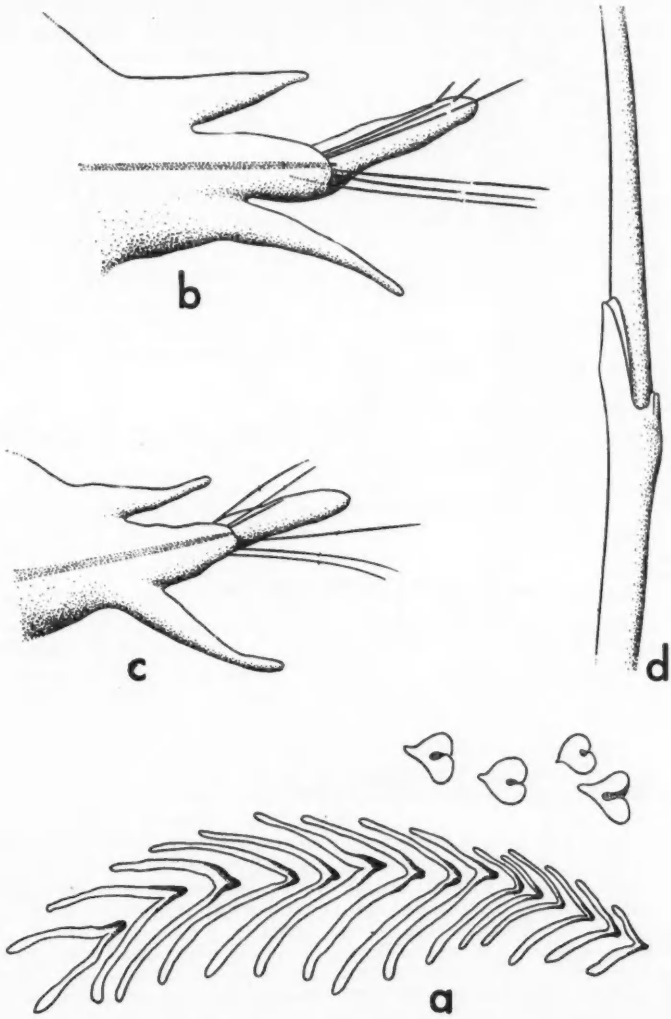

FIG. 1. *Progoniada simplex* n.sp.: (*a*) proboscidial chevron and adjacent papillae, ×411; (*b*) parapodium 18, in posterior view, ×115; (*c*) parapodium 95, in posterior view, ×115; (*d*) articulation of composite spiniger, from parapodium 95, ×1280.

species of the genus, in lacking composite falcigers. Proboscidial chevrons are inconspicuous. The first comes from the Mozambique basin, the second from the northwest Atlantic Ocean, from 770–5001 m.

ONUPHIDAE: onuphid, station 382C (2), 4886–5069 m.

ORBINIIDAE : *Berkeleyia profunda* n.gen., n.sp.

Fig. 2

Record — Station 382C (1, type), 4886–5069 m.

Description — Characters of the genus are those of the species. Single specimen is an anterior fragment

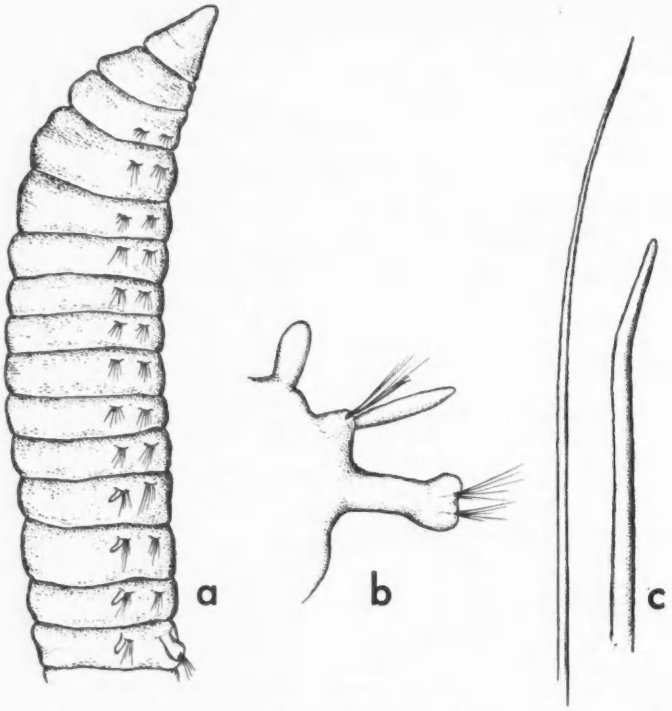

FIG. 2. *Berkeleyia profunda*, n.sp.: (*a*) anterior end in right lateral view, ×28; (*b*) eighth abdominal parapodium in anterior view, ×137; (*c*) superior and inferior setae from eighth abdominal parapodium, ×914.

11 mm long for 30 setigers; 1.3 mm wide in the thorax or widest part. Consists of 12 thoracic and 18 abdominal setigers; posterior end missing. Prostomium conical, slightly depressed, longer than wide, and lacks eyes. A pair of nuchal depressions visible at the sides of the lobe, in line with the linear series of parapodia. Partly everted proboscis is collapsed. First segment is a smooth ring, narrowest in front and widening posteriorly where it joins the first setiger (Fig. 2*a*). All segments smooth, uniannular, and have lateral parapodia.

First 9 setigerous segments largest; their setal fascicles spreading, with notopodia and neuropodia well separated from each other. Next three diminish in size; each has a small notosetal lobe behind the setae and directed dorsally; lobes continue posteriorly with increasing size through the abdominal region, where they are foliose and extend distally beyond setal tips. Thoracic notopodia and neuropodia low ridges throughout. Thoracic setae camerated capillary, with long, tapering tips widest subdistally; camerations formed by internal oblique striations.

Abdominal notopodia low papillar, each with a postsetal foliose lobe; 3 or 4 long slender setae, and 1 or 2 furcate spines emerge from the lobe; most are distally damaged. Abdominal neuropodia longer than notopodia, distally expanded, and weakly incised (Fig. 2*b*); they support 2–4 slender capillary setae and 2 thicker acicular falcigers (Fig. 2*c*). Ventral cirri absent.

Branchiae limited to the abdomen as inconspicuous, simple lobes attached a short distance above the notopodial base; the two of a segment widely separated medially.

The generic and specific characters may be summarized: body consists of 12 thoracic and more numerous abdominal setigers. Change from thorax to abdomen abrupt, marked by a change in neuropodia from low ridges to prolonged lobes. First visible segment a smooth ring longer than the next or first setiger. Proboscis epithelial and pouchlike. Thoracic setae camerated capillary only. Abdominal neuropodia armed with acicular falcigers. Branchiae limited to small, simple, inconspicuous lobes on some abdominal segments. The genus belongs to the ORBINIINAE.

Remarks — *Berkeleyia* is allied to *Haploscoloplos* Monro 1933, in having only camerated capillary

setae in thoracic parapodia, and to *Leodamas* Kinberg 1866, in having acicular falcigers in abdominal neuropodia. It differs from *Schroederella* Laubier 1962, in having two, instead of one anterior smooth segment; thoracic neuropodia lack, instead of have, falcigers.

It is a pleasure to name the genus for Dr Cyril Berkeley, who has had a long, distinguished career concerned with polychaetous annelids, particularly with those from the Pacific area.

CHAETOPTERIDAE: *Phyllochaetopterus* sp., station 369C (1), 2241–2104 m.

CIRRATULIDAE: ?*Chaetozone* sp., station 382C (fgm), 4886–5069 m; *Tharyx* sp., station 386D (1), 4983 m.

FLABELLIGERIDAE : *Ilyphagus* sp.

Record — Station 363B (1), 2954 m.

Description — Body long, linear, 35 × 2.5 mm; consists of at least 28 setigers. Anterior 8 and posterior 9 segments shorter than wide and have the longest setae; median segments cylindrical and longer than wide, armed with characteristic short setae. Surface of the body encrusted with minute orbicular foraminiferans. The few setae of the first setiger longest and directed forward, about as far as the length of the first 6 setigers. Farther back, setae are directed laterally. All are blade-like and cross-striated, beyond their emergence from the parapodium; each tapers abruptly to a slender slightly curved tip; at their greatest width they are closely cross-striated, the striations unusually close-spaced; striations continue distally to the tip. Shortest setae are in posterior neuropodia.

Remarks — This resembles *Ilyphagus hirsutus* Monro (1937 p. 305) from the South Arabian Sea in its setal characters. The two differ in that the first has a long linear body encrusted with foraminiferans, whereas the second has a short sack-likebody, thickly covered with dense, long, cirriform papillae. The setal striations are more crowded and continue more distal in the first than in the second.

FAUVELIOPSIDAE n.fam.

This family is erected to include several flabelligerid-like genera previously referred to FLABELLIGERIDAE. The two differ in that the first lacks a cephalic cage and retractile oral branchiae, characteristic of the second family. Four genera are included: *Fauveliopsis* McIntosh 1922, with type *F. challengeriae* McIntosh, from Antarctic regions, 3566 m; *Flabelligella* Hartman 1965, with type *F. papillata* Hartman, from the northwest Atlantic Ocean, from abyssal depths; *Flota* Hartman 1967, with type *F. flabelligera* Hartman, from off southwestern Chile, from abyssal depths; *Bruunilla natalensis*, new genus and species, see below.

Key to Genera

1. Palpi retractile into the oral cavity; setae present 2
   Palpi absent or not retractile; setae absent 3
2. Neuropodia with composite falcigers ..... *Flabelligella*
   Neuropodia with simple falcate setae ..... *Fauveliopsis*
3. Body enclosed in a thick, translucent, mucoid sheath; bathypelagic ..... *Flota*
   Body without thick, translucent, mucoid sheath; benthic ..... *Bruunilla*

Bruunilla natalensis n.gen., n.sp.

Fig. 3

Record — Station 382C (Fig. 3) (1, type), 4886–5069 m.

Description — The characters of the genus are those of the species. Body smooth, gray, without segmental lines or surface papillae; widest in front and depressed through setigers 3–6, where it is also firmest through the presence of a muscular pharynx. Posterior end tapers to a slender pygidium. Measures 9 × 1.8 mm at most; 16 segments (Fig. 3*a*). Prostomium small plain lobe, more or less concealed by the surrounding peristomium; anterior margin weakly trilobed and lacks eyes. Five cirriform tentacles inserted at the anterior end of the peristomium; median one slightly in front of others; each long, slender, and smooth.

Anterior ventrum has a pair of palplike flat pads extending back through the second setiger; posterior ends are prolonged along the outer side as tapering processes (Fig. 3*b*). Oral aperture depressed between the palpi. Muscular pharynx could not be dissected because of the fragile condition of the single specimen; probing disclosed no chitinized jaws. A pair of widely spaced neural cords visible on the ventrum.

Parapodia lateral and biramous; smaller notopodium tapers to an acute tip and is penetrated by a translucent aciculum. First parapodium has a greatly prolonged ventral cirrus (Fig. 3*c*) and a minute papillar dorsal cirrus. Second parapodium has an enlarged dorsal cirrus with broad base and an inconspicuous ventral cirrus (Fig. 3*d*). Typical neuropodia large, distally truncate

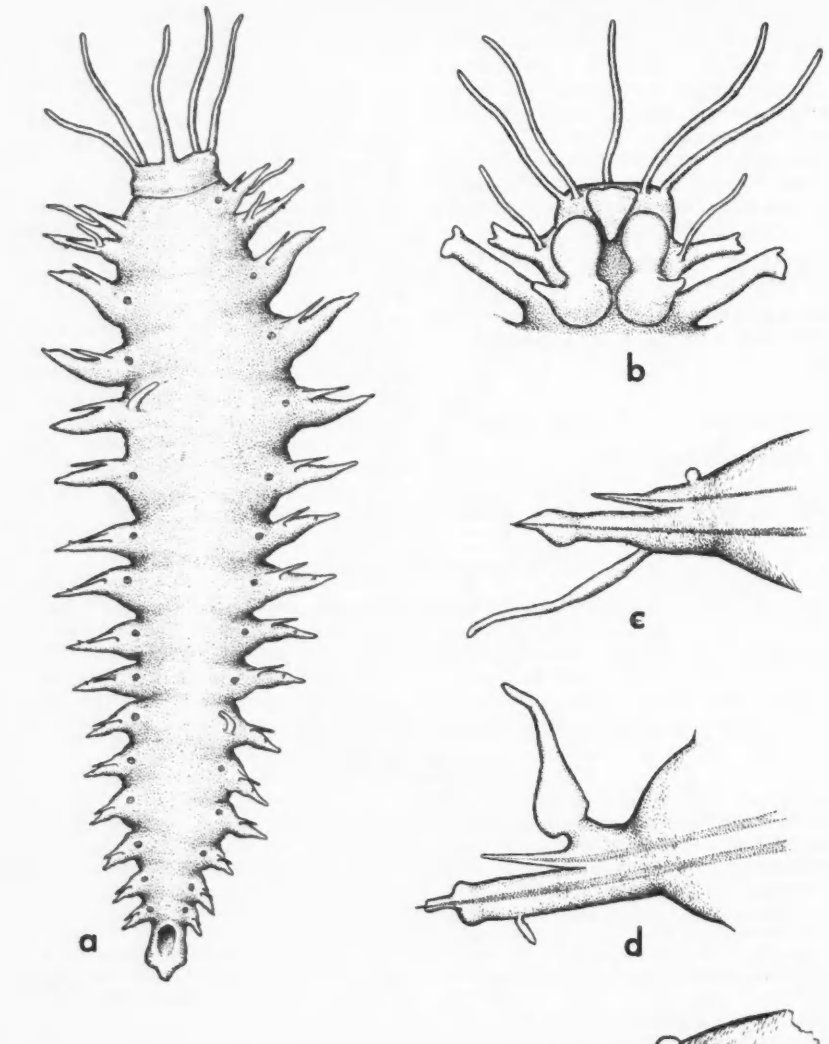

FIG. 3. *Bruunilla natalensis* n.gen., n.sp.: (*a*) outline of entire body, in dorsal view, ×9.1; (*b*) anterior end through first two segments, in ventral view, ×13.6; (*c*) first parapodium from left side, in posterior view, ×22.8; (*d*) second parapodium from right side, in anterior view, ×22.8; (*e*) seventh parapodium, in anterior view, ×22.8; (*f*) basal end of neuro-aciculum showing transverse bars, ×22.8).

or weakly incised (Fig. 3*e*) with a posterior superior part prolonged.

Embedded aciculum a straight, tapering rod, basal end projecting through several segments so that the bases of the two in a segment overlap; they are cross-striated (Fig. 3*f*). Setae totally lacking. Parapodia have long dorsal cirri on setigers 2, 5, and 11, and short papillar cirri on other parapodia. Ventral cirri long, cirriform on the first setiger, then short, simple farther back. Posterior end terminates in a lobed process with a large anal pore opening dorsally.

Remarks — *Bruunilla* is characterized in having a short depressed body consisting of nine segments. Parapodia are subbiramous, consisting of conspicuous neuropodia and reduced notopodia; acicula are present and setae absent. The prostomium is fully exposed. A pair of short thick pads may represent nonretractile palpi. The peristomium is accompanied by two pairs of lateral and a median tentacle. The genus is allied to the FLABELLIGERIDAE in having cross-striated acicula. It differs from all other known polychaetes in its unique cephalic structures.

Bruunilla is named for the R/V *Anton Bruun*, from which the collection was made; the species is named for its origin from the Natal region off southeast Africa.

Fauveliopsis sp.

Record — Station 363D (fgm), 376D (6), 2931 and 4983 m.

Description — Complete specimen from station 376 D slender, slightly coiled, measures 5–7 × less than 1 mm. Body widest in the first 7 setigers, then slender, cylindrical to the posterior truncate end. Cuticle smooth or scabrous, without papillae except for 1 in each interramal space, between notopodia and neuropodia. First 7 setigers shortest and broadest, strongly arched dorsally. Small, inconspicuous prostomium followed by the oral aperture shoved ventrally. First visible segment has setae in biramous fascicles.

Setae are of one kind, acicular, slightly falcate; occur 2-5 in a ramus in anterior parapodia, and 1 or 2 in posterior parapodia; companion capillary setae absent.

Remarks — This differs from *Fauveliopsis arabica* Hartman (1971) in having fewer segments (21–25 instead of 50–86); the first has only acicular falcate setae whereas the second has falcate setae with companion capillary setae. The present records may represent an unnamed species.

Flabelligella ?minuta Hartman

Record — Station 361G (1), 2723 m.

Diagnosis — Body small, white, spinose, oval to disklike; measures 4 × 0.4 mm and consists of 10 setigers. Projecting setae extend laterally. Epithelium is covered with long slender papillae, thickly matted with slender sponge spicules. The first setiger has prolonged simple setae directed forward. Setigers 2–4 have thicker simple setae directed obliquely forward. More posterior setae are more slender and directed laterally. Notosetae are simple and neurosetae composite; each has a long appendage with shaft cross-barred (Fig. 3*g*); appendage long, slender, distally falcate.

Remarks — This was first named (Hartman 1965 p. 176) from off New England, 400 m. The present specimen agrees with the type insofar as its characters can be ascertained.

SCALIBREGMIDAE: *Scalibregma inflata* Rathke 1843, station 368C (1), 2943 m.

OPHELIIDAE : *Ammotrypane brevibranchiata* Caullery 1944

Record — Station 382C (3), 4886–5069 m.

Diagnosis — Length 20 × less than 0.5 mm, setigers 31. Long conical prostomium prolonged forward as a slender palpode nearly as long as the prostomium. The first pair of parapodia is small, located slightly behind the line indicating the oral slit. First 3 setigers lack branchiae; next 3 have long cylindrical branchiae and thereafter the branchiae are abruptly and uniformly small, papillar, continued posteriorly to the second last setiger. Body terminates in a smooth tube longer than the last 2 setigers and crossed by 7 clear rings preceding the short truncate pygidium.

Remarks — This was first named from the East Indies from 1570 m (Caullery 1944 p. 45). The present record is far to the south in the Mozambique basin.

Ammotrypane sp., station 363D (fgm), 2931 m.

MALDANIDAE : *Nicomache* sp.

Record — Station 369(C) (fgm) and 376D (2), 2241–2104 and 4983 m.

Diagnosis — The best preserved is an incomplete specimen, from station 369 C, measuring 61 mm long for 11 setigers. Each segment long, cylindrical, and smooth. First 4 setigers have yellow acicular spines numbering 1–3 in a fascicle; farther back the neuropodia have rostrate setae.

OWENIIDAE : *Myriochele* spp.

Record — Station 366C (8 tubes), 2207 m; 367C (tube), 3349 m; 369C (tubes), 2104 m; 376D (2), 4983 m; 377C (2), 4867 m; 382C (2 tubes), 5069 m; 384C (1), 5490 m; 388C (tube), 3074 m.

Remarks — Most records refer to slender, tapering tubes; no complete specimens are available; median fragments are characterized by the compact, seried rows of long handled uncini.

SABELLARIIDAE: ?*Monorchos* sp., station 376D (2), 4983 m.

Phalacrostemma elegans Fauvel 1911, station 376D (5), 4983 m; 377C (1), 4867 m; 384C (3), 4867–5490 m.

AMPHARETIDAE : *Anobothrus* sp.

Record — Station 363D (2), 2931 m.

Remarks — Two small fragments, each enclosed in a long, cylindrical, silt-covered tube, measure less than 10 mm long for 17 setigers. Paleal fascicles are conspicuous, each in a fanlike series. Setiger 13 is shoved dorsally as characteristic of the genus.

Ampharetids, Not Indentifiable

Record — Station 361G (1); 369C (1); 376D (2), 2104–4983 m.

Remarks — Incomplete specimens from station 376D measure to 5.5 mm long; the anterior end has well-developed paleae as in *Amphicteis*, and four pairs of long slender branchiae inserted in a transverse row.

TEREBELLIDAE : *Axionice ?spinifera* (Ehlers 1908)

Record — Station 376D (fgm) in 4983 m.

Remarks — A short anterior fragment was removed from a long tube measuring 25 mm long. Thoracic uncini of anteriormost segments lack a long shaft. The tube is spiralled, constructed of a series of transverse rings strengthened by minute quartz particles, as typical of the species known from antarctic latitudes (Ehlers 1908 pl. 20).

Terebellid: Station 382C (fgm), 4886–5069 m.

SABELLIDAE : *?Potamethus* sp.

Record — Station 382C (1), 4886–5068 m.

Description — Long silt-covered tube measures 43 × 1.3 mm and contains an animal measuring 7 mm long, without crown, which is 3 mm long. Crown and collar damaged. Radioles about 8 pairs; each has a thick rachis and slender pinnules without eyes. Body consists of 8 thoracic and 10 abdominal setigers; terminates in a blunt end with wide open anal pore. Thoracic setae of two kinds: collar setae long, slender, capillary, in a tuft surpassing other setae in length. Setigers 2–8 have up to 12 superior capillary notosetae and as many inferior bilimbate shorter setae with long slender mucron. Thoracic neuropodia have long-handled avicular uncini, up to 14 in a row. Pennoned setae lacking, hence the questionable generic name.

Abdominal notopodia have short-stemmed avicular uncini as in SABELLINAE; up to 8–14 in a row; each has a beak with large fang surmounted by a crest of many slender teeth; base nearly at right angles to shaft and shorter than erect stalk supporting the crest. Abdominal neuropodia have long, very slender, capillary setae, sparse in a fascicle.

Remarks — The individual has the characteristics of FABRICIINAE in lacking pennoned setae, but also those of SABELLINAE in having avicular abdominal notosetae.

SERPULIDAE : *?Serpula* sp.

Record — Station 363B (fgm), 2954 m.

Remarks — The fragment measures about 4 mm long and lacks a posterior end. A damaged operculum resembles the funnel-like form of *Serpula*. Collar setae have a thick knob subdistally and terminate in a slender tip.

Station List of R/V *Anton Bruun* Cruise 7, Mozambique Basin, 1964

This list gives localities, depths of bottom, and kinds of gear used to recover the samples. Kinds and numbers of metazoan animals are listed for each station. The polychaetes are more completely characterized above.

361E. Aug. 2, 25°50′E, 37°11′S, 2700 m. Campbell grab took about a quart of pale brown clay with foraminiferans. No visible metazoan life.

361G. Aug. 2, 25°50′S, 37°21′E, 2750 m. Menzies trawl took globigerina ooze and muddy clay, bag recovered about half filled with ooze and pteropod shells. Polychaetes: ampharetid; *Flabelligella ?minuta* (see above). Mollusks: gastropod (3); pelecypod (1). Echinoderm: prickly white holothuroid (1). Crustaceans: amphipods (several); arcturid (1); anthurid (1); cumacean (1).

361H. Aug. 3, 25°39′S, 37°45′E, 3750 m. Campbell grab took 0.15 m³ of pale brown mud, globigerina ooze; no visible metazoan life.

362B. Aug. 3, 24°57′S, 39°24′E, 3556–3570 m. Rock-dredge recovered empty, perhaps washed out. No visible metazoan life.

362D. Aug. 4, 24°18′S, 41°26′E, 3934 m. Campbell grab lowered twice, noted strong current from northwest at 2000 m, and increasing at 3200 m; recovered three pints of yellow-brown ooze; no visible metazoan life.

363B. Aug. 5, 23°45′S, 43°10′E, 2980 m. Campbell grab filled with globigerina ooze and brown clay. Polychaetes: ampharetid tube; *Ilyphagus* sp., ?*Serpula* sp. Mollusk: *Malletia* (3). Crustacean: isopod (1 small white). Echinoid (1). Foraminiferans: *Aegerella, Ammodiscus, Cyclamina, Rhabdamina, Rheofax nodolosus*.

363D. Aug. 5, 23°45′S, 43°11′E, 2931 m. Menzies trawl took globigerina ooze. Polychaetes: *Ammotrypane* sp.; *Anobothrus* sp.; *Fauveliopsis* sp. Coelenterate: pennatulid (1). Mollusks: *Limopsis* sp. (3); *Malletia* (several); *Zylophaga* (4). Echinoderms: echinoid (1); ophiuroid, long armed, smooth, flesh colored (1); ophiuroid, small white (1). Crustaceans: amphipod (1); bright red shrimp (1); stalked barnacle (1).

366A. Aug. 13, 23°09′S, 43°09′E, 2300 m. Campbell grab took globigerina ooze; no visible metazoan life.

366C. Aug. 13, 23°09′S, 43°07′E, 2707–2710 m. Agassiz trawl took light brown clay with globigerina ooze; no visible metazoan life; dead tubes of *Myriochele*.

367C. Aug. 14, 22°37′S, 41°22′E, 3250–3349 m. Menzies trawl took globigerina ooze and manganese nodules. Echinoderm: long-armed ophiuroid (1).

367E. Aug. 14, 22°14′S, 40°19′E, 2196–2220 m. Rock-dredge recovered rocks; no visible metazoan life.

367F. Aug. 15, Near Europa Island. 22°12.8′S, 40°38′E, 2750–3808 m. Rock-dredge recovered rock; no metazoan life.

367G. Aug. 15, 22°42′S, 39°19′E, 3140 m. Campbell grab recovered globigerina ooze; no metazoan life, except tube of *Myriochele*.

367J. Aug. 15, 22°38′S, 39°24′E, 3038–3040 m. Agassiz trawl recovered empty.

368C. Aug. 16, 23°00′S, 38°38′E, 2995 m. Menzies trawl 45 min on bottom; took ooze and nodules and diversified invertebrates. Bryozoan: long slender branches and attached rhizome (1). Polychaete: *Scalibregma inflata*. Crustaceans: caprellid (1); isopod (1).

369C. Aug. 17, 23°48′S, 37°45′E, 2104–2241 m. Agassiz trawl took globigerina ooze and diversified animals. Bryozoan: long slender branches with attached rhizome (1). Coelenterate: pennatulid (1). Polychaetes: ampharetid; *Nicomache* sp., phyllochaetopterid; sipunculid (1). Echinoderms: asteroid, small white disk (1); echinoid (2); holothuroid, prickly white (1); holothuroid, smooth pink (1); ophriuoid (2). Crustaceans; red shrimp (1); ?*Steriomastus* crab (1); *Scalpellum* barnacle attached to pennatulid (1).

375G. Aug. 25, 29°06′S, 36°44′E, 3879–3890 m. Rock-dredge took clay and manganese nodules; no visible metazoan life.

376B. Aug. 26, 29°26′S, 37°35′E, 4860 m. Rock-dredge took rocks and mud; no visible metazoan life.

376D. Aug. 26, 29°20′S, 37°26′E, 4983–5000 m. Menzies trawl took red clay and diversified animals. Bryozoan, branching white, attached to hard surface (1). Polychaetes: ampharetid; ?*Aphrodita* sp.; *Axionice* ?*spinifera*; *Euphrosine* sp.; *Fauveliopsis* sp.; *Glycera* ?*papillosa*; *Monorchos* sp.; *Nicomache* sp.; *Myriochele* sp.; *Phalacrostemma elegans*; sphaerodorid; *Tharyx* sp. Echinoderms: asteroid, small white disk (1); ophiuroid (fgm). Crustaceans: amphipod (several); tanaid (1); cumacean (1).

377C. Aug. 27, 30°12′S, 38°35′E, 4867–4870 m. Menzies trawl in clay bottom. Polychaetes: *Myriochele* sp; *Phalacrostemma elegans*. Crustacean: phyllosomid larva (1).

379D. Aug. 29, 32°27′S, 43°00′E, 2397–2400 m. Rock-dredge took globigerina ooze. Echinoderm: ophiuroid (2 fgm).

382C. Aug. 31, 34°06–10′S, 41°14–15′E, 4886–5069 m. Menzies trawl took red-brown mud. Polychaetes: *Ammotrypane brevibranchiata*; *Berkeleyia profunda*; *Bruunilla natalensis*; ?*Chaetozone* sp.; lacydonid; *Myriochele* sp; onuphid; *Progoniada simplex*; ?*Potamethus* sp.; terebellid. Mollusk (1). Crustaceans: amphipod (several); isopod (1); cumacean (1).

383C. Sept. 1, 34°45′S, 38°47′E, 5250 m. Menzies trawl recovered a cupful of brown clay. Coelenterate: hydroid. Mollusks: *Abra* (2); gastropod (3). Crustaceans: amphipod (1); isopod (1); tanaid (1).

384C. Sept. 3, 35°51′S, 36°46′E, 5490–5450 m. Agassiz trawl took clay and manganese nodules. Coelenterate: ?anemone (1). Bryozoan: branching white, attached to hard surface. Polychaetes: *Myriochele* sp; *Phalacrostemma elegans*. Mollusks: pelecypod (1); gastropod (1).

387C. Sept. 5, 31°54′S, 34°21′E, 2562–2700 m. Rock-dredge took ooze and manganese nodules. Sponge: foliose white (several). Echinoderm: ophiuroid, long-armed (1).

388C. Sept. 6, 30°49–55′S, 32°58′E, 3074–3090 m. Agassiz trawl took globigerina ooze with animals. Sponge: small black sphere (1). Coelenterates: pennatulid (1); hydrozoan as in 376D (1). Brachiopod: ?*Terebratalia* (1). Polychaete: *Myriochele* sp. Mollusks: gastropod (1); *Zylophaga* sp. (4). Echinoderms: asteroid, small white disk (1); short-armed ophiuroid, coral colored (2). Crustaceans: anthurid (1); tanaid (1); ?cumacean (1); dorippid crab (1).

Compendium of Abyssal Polychaetous Annelids from World-Wide Areas, With Bibliographic Citations

Abyssal polychaetes, or those named from depths of 2000 m or more, number about 504 species in 242 genera and 52 families. Best represented are the families AMPHARETIDAE, 54 species in 30 genera; POLYNOIDAE, 48 species in 17 genera; MALDANIDAE, 36 species in 17 genera; ONUPHIDAE, 29 species in 6 genera; TEREBELLIDAE, 27 species in 16 genera; LUMBRINERIDAE, 22 species in 3 genera; and OPHELIIDAE, 20 species in 6 genera.

Each of the 52 families is known for species from shallower depths except FAUVELIOPSIDAE, which is almost exclusively abyssal. On the generic level it can be concluded that most occur in shallow to great depths; only about 75 genera, or 30% of the total number, are largely or wholly abyssal; they are preceded by an asterisk (*) in the following

list of species. Most of the species named are limited to great depth; a few have a range extending through Indo-Pacific areas, and fewer than 50, or 10%, can be regarded as cosmopolitan or eurybathic in occurrence.

Bibliographic citations refer to abyssal records.

APHRODITIDAE, with 8 species in 2 genera

Aphrodita aculeata Linnaeus. Gulf of Gascony and northwest Atlantic Ocean from depths to 2750 m (Fauvel 1914 p. 33; Ditlevsen 1937 p. 55; Hartman 1965 p. 49).

Aphrodita talpa Quatrefages. Bering Sea, to 2995 m (Levenstein 1961a p. 151).

Aphrodita sp. Mozambique basin, 4982 m (see above).

Laetmonice batheia Horst 1916 p. 75. Off Malay, 2798 m.

Laetmonice filicornis Kinberg. Off Azores and northwest Atlantic Ocean, to 3200 m (Fauvel 1914 p. 34; Ditlevsen 1937 p. 55; Hartman 1965 p. 49).

Laetmonice filicornis benthaliana McIntosh 1885 p. 45. Australian Antarctic Ocean, 3566–5303 m.

Laetmonice producta willemoesi McIntosh 1885 p. 47. Between Azores and Antarctic Ocean, 3064 m.

Laetmonice producta wyvillei McIntosh 1885 p. 44. Between Australia and Antarctica, to 3752 m; off Peru, 3120 fath (Chamberlin 1919 p. 82).

POLYNOIDAE, with 48 species in 17 genera

**Admetella longipedata* McIntosh. North Atlantic Ocean, 5025 m (Eliason 1951 p. 143).

**Antinoana fusca* Hartman and Fauchald 1971 USC. Northwest Atlantic Ocean, to 4680 m.

Antinoella badia (Theel). Off Greenland, to 3521 m (Ditlevsen 1937 p. 55).

Austrolaenilla abyssicola (Uschakov 1962 p. 172). Eastern sector of Antarctica, 4540 m.

Austrolaenilla antarctica Bergstroem. Scotia Sea and South Orkney Islands, Antarctica, to 2818 m (Hartman 1967 p. 19).

**Bathymoorea renotubulata* (Moore 1910 p. 368, as *Polynoe*). West off Santa Catalina Island, California, to 4074 m (Pettibone 1967 p. 10).

Eunoe abyssorum McIntosh 1885 p. 73. Off southern Australia, 4755 m.

Eunoe eura Chamberlin 1919 p. 58. Off Peru, 5706 m.

Eunoe iphionides McIntosh 1885 p. 69. New Zealand sector of Antarctica, to 3817 m.

Eunoe macrophthalma McIntosh 1924 p. 7. Off South Africa, 2160 m.

Eunoe cf. *spinulosa* Verrill. Off New England, 2886 m (Hartman and Fauchald 1971 p. 23)

Harmothoe bathydomus Ditlevsen 1917 p. 25. Off southern Greenland, 3230 m.

Harmothoe benthaliana McIntosh 1885 p. 95. Off New York, 2257 m.

Harmothoe benthophila Ehlers 1913 p. 444. Cape Verde Island, over 3000 m.

Harmothoe crosetensis (McIntosh 1885 p. 88). Crozet Islands, Antarctica, 2912 m.

Harmothoe echinopustulata Fauvel 1913 p. 19. Off France, 2000 m.

Harmothoe globefera (Sars). North Atlantic Ocean, 3520 m (Eliason 1951 p. 143).

Harmothoe johnstoni (McIntosh). Gulf of Gascony, abyssal (Fauvel 1914 p. 61).

Harmothoe spinosa Kinberg. Antarctic Ocean, 3397 m (Ehlers 1913 p. 438).

Harmothoe tenuisetis (McIntosh 1885, as *Evarne*). Off Strait of Gibraltar, 2275 m.

**Herdmanella ascidioides* (McIntosh 1885 p. 109). South of Australia, 4755 m.

Herdmanella nigra Hartman 1967 p. 25. South Sandwich Islands, Antarctica, 2553–2575 m.

Hololepidella flynni Benham 1921 p. 33. South of Tasmania, Australia, 2340 m.

Hyperhalosydna striata (Kinberg). Bass Strait, Australia, 4024 m (McIntosh 1885 p. 111, as *Polynoe platycirrus*).

Lagisca (*Agnidice*) *moseleyi* McIntosh 1885 p. 87. Off Sierra Leone, mid-Atlantic Ocean, 3385 m.

Lagisca hubrechti McIntosh. North Atlantic Ocean, abyssl (Fauvel 1914 p. 67).

Lagisca oculata Hartman 1967 p. 29. Weddell Sea, Antarctica, 2818–2846 m.

Lagisca peracuta McIntosh. Off Morocco, abyssal (Fauvel 1914 p. 67).

**Lepidofimbria oculata* Hartman 1967 p. 32. Weddell Sea, 2818–2846 m.

**Lepidogyra alba* Hartman 1967 p. 33. Weddell Sea, 2818–2846 m.

**Macellicephala abyssicola* Fauvel 1913 p. 7. Gulf of Gascony, 4380 m. Kermadec trench, 6620–7000 m (Levenstein 1961a p. 151).

Macellicephala affinis Fauvel 1914 p. 7. Off Madeira, over 2380 m.

Macellicephala bicornis Levenstein 1962 p. 1143. Tonga trench, 9875–9735 m.

Macellicephala eltanina Hartman 1967 p. 34. South Sandwich Islands, Antarctica, 2553–2575 m.

Macellicephala ?incerta Fauvel 1915 p. 1. Off Azores, over 3000 m.

Macellicephala hadalis Kirkegaard 1956 p. 64. Kermadec and Banda trenches, 8210–8300 m.

Macellicephala longipalpa Uschakov 1957 p. 1663. Arctic Ocean, 2245 m.

Macellicephala macrophthalma Fauvel 1913 p. 9. Gulf of Gascony, 4780 m.

Macellicephala mirabilis McIntosh. North Atlantic Ocean, abyssal (Eliason 1951 p. 143).

Macellicephala nationalis (Ehlers). Off southern South America, in 3806 m (Hartman 1967 p. 36).

Macellicephala polaris Uschakov 1957 p. 1664. Arctic Ocean, 2445 m.

Macellicephala zenkevitchi Uschakov 1955a p. 313. Northwest Pacific Ocean, 8100 m.

**Macellicephaloides grandicirra* Uschakov 1955a p. 314. Northwest Pacific Ocean, 8100–9950 m.

Macellicephaloides verrucosa Uschakov 1955a p. 316. Northwest Pacific Ocean, 7210–7231 m.

Macellicephaloides vitiazi Uschakov 1955a p. 318. Northwest Pacific Ocean, 7210–8430 m.

**Macellicephaloides* sp. Levenstein 1962 p. 1143. Tonga trench, 10,630–10,710 m.
**Robertianella synopthalma* McIntosh 1885 p. 122. Between Canary Islands and Brazil, 2912 m.
**Weberia nodulosa* (Ditlevsen 1917 p. 42). Off Iceland, 1089 fath.

SIGALIONIDAE, with 7 species in 4 genera

Leanira abyssicola (McIntosh 1879 p. 501). Mid-North Atlantic Ocean, 3264 m.
Leanira hystricis Ehlers 1874 p. 292. North Atlantic Ocean, to 1443 fath.
Leanira minor Hartman 1965 p. 52. North Atlantic Ocean, to 4540 m.
Leanira quatrefagesi Kinberg. Scotia Sea, Antarctica, to 4758 m (Hartman 1967 p. 40).
Pholoe anoculata Hartman 1965 p. 52. Off New England, to 5000 m.
Sthenelais sp. Hartman and Fauchald 1971 p. 27. Off Bermuda and northwest Atlantic Ocean, to 2802 m.
Sthenolepis tetragona (Oersted). Off Azores, 2139 m (Fauvel 1914 p. 85).

PISIONIDAE, with 1 species

**Pisionura abyssorum* Hartman and Fauchald 1971 p. 33. North Atlantic Ocean, 5018–5023 m.

CHRYSOPETALIDAE, with 1 species

Dysponetus gracilis Hartman. Northwest Atlantic Ocean, to 2802 m (Hartman and Fauchald 1971 p. 34).

AMPHINOMIDAE, with 5 species in 4 genera

Chloeia sp. Off Bermuda Islands, to 2223 m (Hartman and Fauchald 1971 p. 34).
Chloenea atlantica McIntosh 1885 p. 15. Off Canary Islands, 2775 m.
Paramphinome australis Monro. South Orkney Islands and Bransfield Strait, Antarctica, to 2818 m (Hartman 1967 p. 44).
Paramphinome jeffreysii (McIntosh). North Atlantic Ocean, to 2900 m (Hartman 1965 p. 58).
Pseudeurythoe cf. *ambigua* (Monro). Velero basin, California, 2115 m (Hartman 1960 p. 270).

EUPHROSINIDAE, with 2 species in genus

Euphrosine lanceolata McIntosh 1876 p. 395. Off Ireland, 3364 m.
Euphrosine sp. Northwest Atlantic Ocean and Mozambique basin (see above).

PHYLLODOCDIAE, with 13 species in 10 genera

Anaitides sp. Northwest Atlantic Ocean, to 3806 m (Hartman and Fauchald 1971 p. 36).
**Austrophyllum charcoti* (Gravier). Antarctica, 4773 m (Hartman 1967 p. 48).
Austrophyllum maculatum Hartman and Fauchald 1971 p. 38. Northwest Atlantic Ocean, 4680 m.
Eteone rarica Uschakov 1958 p. 204. Off Kamchatka, Bering Sea, 5070 m.
Eulalia sphaerocephala Levenstein 1961a p. 150. Bering Sea, 2440–3680 m.
Eulalia sp. Hartman 1967 p. 50. American sector of Antarctica, 5918 m.
Eumida sp. Hartman 1967 p. 51. Peter I Island, Antarctica, 4503 m.
Notophyllum coecum Fauvel 1913 p. 52. Off Azores, 5005 m.
Paranaitis wahlbergi (Malmgren). Off New England, 4950 m (Hartman 1965 p. 62).
**Pirakia lanceolata* Hartman and Fauchald 1971 p. 44. Off New England, 4749 m.
Protomystides bidentata (Langerhans). Off New England, 2000–4950 m (Hartman 1965 p. 62).
Protomystides limbata punctata Hartman 1965 p. 63. Off New England, 4892 m.
Vitiazia dogieli Uschakov 1953 p. 217. Off Kurile Islands, 8100 m.

ALCIOPIDAE, with 1 species

Vanadis crystallina Greeff. North Atlantic Ocean, 5610–5600 m. (Eliason 1951 p. 143).

LACYDONIDAE, with 3 species in 2 genera

Lacydonia papillata Uschakov 1958 p. 206. Kurile Trench, Bering Sea in 5070 m.
Lacydonid. Mozambique basin, see above.
Paralacydonia paradoxa Fauvel. Velero basin, California, 2115 m (Hartman 1960 p. 270).

TYPHOSCOLECIDAE, with 3 species in 2 genera

Travisiopsis coniceps (Chamberlin). Drake Passage, Antarctica, 3678–4136 m (Hartman 1967 p. 52).
?Travisiopsis lanceolata Southern. Off New England, 2469–4540 m, pelagic (Hartman 1965 p. 66).
?Typhloscolex sp. Hartman and Fauchald 1971 p. 49. Northwest Atlantic Ocean, 4743–4893 m.

HESIONIDAE, with 5 species in 5 genera

Castalia punctata, fide Fauvel 1914 p. 122. Gulf of Gascony, 2320 m.
Dalhousiella carpenteri McIntosh 1901 p. 231. Between Ireland and Azores, abyssal.
**Hesiocaeca bermudensis* Hartman 1965 p. 68. Off Bermuda, 2500 m.
Leocrates atlantica (McIntosh 1885 p. 186). Off Canary Islands, 1525 fath.
**Neopodarke woodsholea* Hartman 1965 p. 69. Off New England, 2500 m.

PILARGIDAE, with 5 species in 3 genera

Ancistrosyllis groenlandica McIntosh. Northwest Atlantic Ocean, 2900 m (Hartman 1965 p. 71).

Ancistrosyllis, near *groenlandica* Hartman 1967 p. 53. Off Chile and Drake Passage, Antarctica, 3867–4086 m.

Ancistrosyllis constricta, sensu Kirkegaard 1956 p. 66. Banda trench, 6580 m.

Sigambra tentaculata (Treadwell). Northwest Atlantic Ocean, slope depths to 5001 m (Hartman 1965 p. 71); Velero basin, California, 2115 m (Hartman 1960 p. 270).

Synelmis albini (Langerhans). Northwest Atlantic Ocean, to 2500 m (Hartman 1965 p. 70, as *Ancistrosyllis*).

SYLLIDAE, with 6 species in 5 genera

**Braniella palpata* Hartman 1967 p. 55. Off Cape Horn and Antarctic Peninsula, to 3806 m.

Braniella pupa Hartman. North and mid-Atlantic Ocean, to 4892 m (Hartman and Fauchald 1971 p. 51).

Exogone dispar (Webster). Off New England, to 2900 m (Hartman 1965).

**Exogonita oculata* Hartman and Fauchald 1971 p. 53. Northwest Atlantic Ocean, 3806–4825 m.

Langerhansia anoculata Hartman and Fauchald 1971 p. 54. Off New England, to 2900 m.

Typosyllis sp. Weddell Sea, Antarctica, 2818–2846 m (Hartman 1967 p. 62).

NEREIDAE, with 13 species in 6 genera

Ceratocephale loveni Malmgren. Bering Sea, to 4400 m (Levenstein 1961 p. 155); North Atlantic Ocean, to 5023 m (Hartman 1965 p. 83).

Ceratonereis beringiana Levenstein 1961a p. 153. Bering Sea, to 4400 m.

Ceratonereis versipedata Ehlers. Northwest Atlantic Ocean, in 2802–4769 m (Hartman and Fauchald 1971 p. 58).

Neanthes abyssorum Hartman 1967 p. 63. Bransfield Strait, Antarctica, 2119–2562 m.

Nereis caecoides Hartman 1965 p. 85. Northwest Atlantic Ocean, 2946 m.

Nereis kerguelensis McIntosh. Off Azores, 5005 m (Fauvel 1914 p. 168).

Nereis longisetis McIntosh 1885 p. 222. Strait of Gibraltar, 2775 m.

Nereis profundi Kirkegaard 1956 p. 67. Banda trench, 7250–7290 m.

Nereis zonata Malmgren. Cape Verde Island, Atlantic Ocean, 3899 m (Fauvel 1914 p. 178).

Nereis sp. Java trench, abyssal (Levenstein 1961b p. 136).

Nicon abyssalis Hartman 1967 p. 66. Antarctica Peninsula, 4310–4328 m.

Nicon sp. Hartman and Fauchald 1971 p. 59. Northwest Atlantic Ocean, 3753 m.

Platynereis dumerilii (Audouin and Milne Edwards). North Atlantic Ocean, littoral to 4850 m (Hartman 1965 p. 88).

NEPHTYIDAE, with 9 species in 3 genera

Aglaophamus digitatus Hartman 1967 p. 71. South Sandwich Islands, Antarctica, 2531–2452 m.

Aglaophamus elamellata (Eliason 1951) North Atlantic Ocean, in 4267–4600 m. Kermadec trench, 6620 m (Kirkegaard 1956 p. 68, as *Nephthys*).

Aglaophamus groenlandiae Hartman 1967 p. 73). Off southern Greenland, 3404–3422 m.

Aglaophamus posterobranchus Hartman 1967 p. 78. Off Chile and South Orkney Islands, Antarctica, to 4118 m.

Aglaophamus sp., acirrate. Hartman 1965 p. 91. North Atlantic Ocean, 3742 m.

Micronephthys abrachiata (Ehlers). Kermadec trench, 8928–9174 m (Levenstein 1962 p. 1145, as *Nephtys*).

Nephtys ferruginea Hartman. Shag rocks, Antarctica, 3403–3484 m (Hartman 1967 p. 81).

Nephtys hystricis McIntosh. Off Azores, 2252 m (Fauvel 1914 p. 200), and North Atlantic Ocean, 2500 m (Hartman 1965 p. 92).

Nephtys paradoxa Malm. North Atlantic Ocean, to 2257 m (McIntosh 1885 p. 164, as *Nephtys phyllobranchia*).

SPHAERODORIDAE, with 8 species in 4 genera

**Clavodorum atlanticum* Hartman and Fauchald 1971 USC. Northwest Atlantic Ocean, 3834–4769 m.

**Ephesiella antarctica* (McIntosh 1885 p. 361). Eastern sector of Antarctica, abyssal depths.

Ephesiella macrocirrus Hartman and Fauchald 1971 p. 65. North Atlantic Ocean, 2802 m.

Ephesiella mixta Hartman and Fauchald 1971 p. 66. Northwest Atlantic Ocean, 3753 m.

**Sphaerodopsis elegans* Hartman and Fauchald 1971 p. 71. Mid-Atlantic Ocean, 2886–3783 m.

Sphaerodopsis longipalpa Hartman and Fauchald 1971 p. 72. Northwest Atlantic Ocean, to 2886 m.

Sphaerodorum parvum Ehlers. Antarctic Ocean, to 4758 m (Hartman 1967 p. 87).

Sphaerodorid, unknown species. Mozambique basin, 4983 m (see above).

GLYCERIDAE, with 5 species in 1 genus

Glycera capitata Oersted. North Atlantic Ocean, 3200 m (McIntosh 1879 p. 499).

Glycera fundicola Chamberlin 1919 p. 352. Off Peru, 4063 m.

Glycera mimica Hartman 1965 p. 98. North Atlantic Ocean, slope depths to 5023 m.

Glycera ?papillosa Grube. Mozambique basin, see above.

Glycera rouxii Audouin and Milne Edwards. North Atlantic Ocean and Gulf of Gascony, 4380 m (Fauvel 1914 p. 203).

GONIADIDAE, with 6 species in 3 genera

Glycinde lindbergi Uschakov 1955b p. 176. Okhotsk Sea, 2850 m.

Glycinde profunda Hartman and Fauchald 1971 p. 74. Northwest Atlantic Ocean, 2862–5023 m.
Glycinde sp. Hartman 1967 p. 88. Cape Horn and Drake Passage, to 4008 m.
Goniada sp. Hartman and Fauchald 1971 p. 76. North Atlantic Ocean, 3834–4892 m.
**Progoniada regularis* Hartman 1965 p. 98. North Atlantic Ocean, slope depths to 5023 m.
Progoniada simplex Hartman. Mozambique basin, see above.

ONUPHIDAE, with 29 species in 6 genera

Hyalinoecia benthaliana McIntosh 1885 p. 339. South of Australia, 3292 m.
Hyalinoecia edwardsi Roule 1898 p. 193. Off Azores, 4255 m.
Hyalinoecia stricta Moore 1911 p. 280. Off San Diego, California, abyssal (Hartman 1960 p. 98, as *Hyalinoecia tubicola stricta*).
Nothria abranchiata McIntosh 1885 p. 314. Antarctica, 2452–4041 m.
Nothria abyssalis Fauchald 1968 p. 19. Off Baja, California, Mexico, 1431–1490 fath.
Nothria armandi McIntosh 1885 p. 330. South of Australia, 1950 fath.
Nothria conchylega (Sars). Off Azores, 4020 m (Fauvel 1914 p. 128).
Nothria, near *conchylega* Hartman 1967 p. 90. Antarctic Ocean, slope depths to 3825 m.
Nothria ehlersi McIntosh 1885 p. 327. Off Chile, 4070 m.
Nothria notialis (Monro). Antarctica, to 3752 m (Hartman 1967 p. 92).
Nothria pycnobranchiata McIntosh 1885 p. 317. Off Chile, 4070 m; Bering Sea, 3075 m (Levenstein 1957 p. 286).
Nothria textor Hartman and Fauchald 1971 p. 78, Northwest Atlantic Ocean and Bermuda rise, to 4892 m.
Nothria sp. Hartman 1965 p. 107. North Atlantic Ocean, to 3752 m; Antarctica at Drake Passage, 4172–4209 m (Hartman 1967 p. 93).
Onuphis cobra Chamberlin 1919 p. 300. Off Pacific Panama, 3240 m.
Onuphis lepta Chamberlin 1919 p. 290. Pacific Panama, 2286 m.
Onuphis litabranchia Chamberlin 1919 p. 274. Off western Mexico, 3436 m.
Onuphis pachytmema Chamberlin 1919 p. 279. Off Peru, 4334 m.
Onuphis paucibranchis (Ehlers). Antarctica, 3404–4813 m (Hartman 1967 p. 93).
Onuphis pycnobranchiata McIntosh. Bering Sea in 3875 m (Levenstein 1957 p. 286).
Onuphis socia Chamberlin 1919 p. 284. Off Peru, 4755–5203 m.
Onuphis vexillaria Moore. Velero basin, California, 2115 m (Hartman 1960 p. 270).
Onuphis sp. Off Peter I Island, Antarctica, 3848–3980 m (Hartman 1967 p. 94).
**Paranorthia antarctica* Hartman 1965 p. 94. Weddell Sea, 3285 m.
Paranorthia atlantica Hartman 1965 p. 108. North Atlantic Ocean, 2800–3540 m.
**Paronuphis abyssorum* (Chamberlin 1919 p. 320). Between Peru and Galapagos Islands, 3666 m.
Paronuphis bermudensis Hartman 1965 p. 113. Off Bermuda Islands, to 2500 m.
Paronuphis benthaliana (McIntosh 1885 p. 339). South of Australia, 2366–4813 m.
Paronuphis solenotecton Chamberlin 1919 p. 306. Pacific Panama, 2286 m.
Rhamphobrachium agassizi Ehlers. Off Morocco, 2165 m (Fauvel 1914 p. 126), and North Atlantic Ocean, to 2500 m (Hartman 1965 p. 113).

EUNICIDAE, with 2 species in 1 genus

Eunice collini Augener. Off Morocco, 2165 m (Fauvel 1914 p. 31).
Eunice norvegica (Linnaeus). Off Morocco, abyssal (Fauvel 1914 p. 136); off Greenland in 3229 m (Wesenberg-Lund 1950a p. 66, as *E. pennata*).

LUMBRINERIDAE, with 22 species in 3 genera

**Cenogenus descendens* Chamberlin 1919 p. 333. Off Peru, 2222 fath.
Lumbrineris abyssicola (Uschakov 1950a p. 195). Okhotsk Sea, 3500 m. Bering Sea, 3500–4820 m (Levenstein 1961a p. 156).
Lumbrineris abyssorum (McIntosh 1885 p. 250). Off Peru, 4070 m.
Lumbrineris antarctica Monro. Antarctica, American sector, slope depths to 4758 m (Hartman 1967 p. 100).
Lumbrineris atlantica (Kinberg). Western Atlantic Ocean, 2000–3753 m (Hartman and Fauchald 1971 p. 82).
Lumbrineris bifilaris (Ehlers). Southern California, 3990 m (Moore 1911 p. 291).
Lumbrineris bistriata (Levenstein 1961a p. 157). Bering Sea, 3330–4418 m.
Lumbrineris crassicephala Hartman 1965 p. 17. Northwest Atlantic Ocean, 1102–2823 m.
Lumbrineris ehlersi tenuisetis McIntosh 1885 p. 253. Off New York, 2439 m.
Lumbrineris fragilis (Mueller). North Atlantic Ocean, 3264 m (Hartman 1965 p. 118).
Lumbrineris impatiens (Claparede). Gulf of Gascony, 4380 m (Fauvel 1914 p. 155).
Lumbrineris latreilli (Audouin and Milne Edwards). Northwest Atlantic Ocean, to 4773 m (Hartman and Fauchald 1971 p. 83).
Lumbrineris magalhaensis Kinberg. South Sandwich Islands, Antarctica, to 2531 m (Hartman 1967 p. 101).
Lumbrineris minuscula Moore 1911 p. 294. Off Hawaiian Islands, 3990 m.
Lumbrineris moorei Hartman 1942 p. 116. West off Santa Catalina Island, California, to 2182 fath.
Lumbrineris paradoxa (St. Joseph). Northwest Atlantic Ocean, to 2802 m (Hartman and Fauchald 1971 p. 83).
Lumbrineris punctata (McIntosh 1885 p. 252). Off New York, 2257 m.

Ninoe brevipes (McIntosh 1903) (as *Lumbriconereis*). North Atlantic Ocean, 1102–4825 m (Hartman and Fauchald 1971 p. 85).
Ninoe dibranchia Hartman and Fauchald 1971 p. 86. Northwest Atlantic Ocean, 1102–3834 m.
Ninoe fusca Moore 1911 p. 285. Off Southern California, 4016 m.
Ninoe gayheadia Hartman 1965 p. 121. Northwest Atlantic Ocean, to 4950 m.
Ninoe spp. Northwest Atlantic Ocean, 520–4950 m (Hartman 1965 p. 123); Antarctica, 192–3438 m (Hartman 1967 p. 101).

ARABELLIDAE, with 2 species in 2 genera

Drilonereis zenkevitchi Levenstein 1961a p. 157. Bering Sea, 2995–3330 m.
Laranda longa sensu McIntosh 1885 p. 237. Between Halifax, N.S., and New York, N.Y., 2439 m.

DORVILLEIDAE, with 2 species in 2 genera

Dorvillea rudolphi anoculata Hartman 1965 p. 124. Northwest Atlantic Ocean, 97–2478 m.
Ophryotrocha sp. Northwest Atlantic Ocean, 2022–3753 m (Hartman and Fauchald 1971 p. 91).

ORBINIIDAE, with 14 species in 9 genera

**Berkeleyia profunda* n.gen., n.sp. Mozambique basin, see above.
**Califia calida* Hartman. Velero basin, California, 2115 m (Hartman 1960 p. 270).
Califia chilensis Hartman 1967 p. 102. Off Santiago, Chile, 3655–3651 m.
Califia schmitti (Pettibone). Northwest Atlantic Ocean, 1330–5000 m (Hartman and Fauchald 1971 p. 91).
Haploscoloplos abranchiata Hartman 1967 p. 103. Falkland Islands and Cape Horn, 2452–4008 m.
Haploscoloplos fragilis intermedius Hartman 1965 p. 128. Northwest Atlantic Ocean, 300–3752 m.
Haploscoloplos kerguelensis (McIntosh). Weddell Sea, Antarctica, 2818–3514 m (Hartman 1967 p. 105).
**Microrbinia linea* Hartman 1965 p. 129. Northwest Atlantic Ocean, 196–4680 m.
Naineris quadricuspida (Fabricius). Arctic and North Atlantic oceans, to 2071 m (Ditlevsen 1937 p. 55); Bermuda Islands, 2500 m (Hartman 1965 p. 130).
Orbiniella drakei Hartman 1967 p. 106. Drake Passage, 3312–3532 m.
Phylo norvegicus (Sars). Northwest Atlantic Ocean, 2900 m (Hartman 1965 p. 130).
Scoloplos (*Leodamas*) *marginatus* (Ehlers). South Orkney Islands, Antarctica, 298–2800 m (Hartman 1967 p. 108).
Scoloplos spp. Northwest Atlantic Ocean, 1102–4970 m (Hartman and Fauchald 1971 p. 92).
Orbiniid, unknown. Northwest Atlantic Ocean, 4667 m (Hartman and Fauchald 1971 p. 93).

PARAONIDAE, with 17 species in 6 genera

Aedicira belgicae (Fauvel). Northwest Atlantic Ocean, 300–4950 m (Hartman 1965 p. 135); off southern South America, 2621–4008 m (Hartman 1967 p. 110).
Aedicira parva Hartman and Fauchald 1971 p. 95. Northwest Atlantic Ocean, 530–5000 m.
**Aparaonis abyssalis* Hartman 1965 p. 136. Off New England, 4436 m.
Aricidea fragilis, sensu McIntosh 1885 p. 354. North American east coast, 2439 m.
Aricidea neosuecica Hartman 1965 p. 137. Northwest Atlantic Ocean, 97–2496 m.
Aricidea suecica Eliason, anoculate. Northwest Atlantic Ocean, 97–2496 m (Hartman and Fauchald 1971 p. 97).
Aricidea tetrabranchia Hartman and Fauchald 1971 p. 98. Northwest and mid-Atlantic Ocean, 1102–3753 m.
Aricidea uschakovi, sensu Hartman 1967 p. 110. Drake Passage and off Santiago, Chile, 298–4099 m.
**Paradoneis abranchiata* Hartman 1965 p. 140. Northwest Atlantic Ocean, 2000–4850 m.
Paraonides monilaris Hartman and Fauchald 1971 p. 100. Northwest Atlantic Ocean, 2864–4825 m.
Paraonides rubiceps Hartman and Fauchald 1971 p. 101. Northwest Atlantic Ocean, 1102–3753 m.
Paraonis coronatus Hartman 1965 p. 141. Northwest Atlantic Ocean, 400–2946 m.
Paraonis gracilis (Tauber). Northwest Atlantic Ocean, 97–2752 m (Hartman 1965 p. 141); Velero basin, California, 2115 m (Hartman 1960 p. 270).
Paraonis gracilis, aristate, Hartman 1965 p. 142. Northwest Atlantic Ocean, to 3753 m.
Paraonis reductus Hartman 1965 p. 142. Northwest Atlantic Ocean, 1102–5007 m.
Paraonis uncinatus Hartman 1965 p. 143. Northwest Atlantic Ocean, 530–4892 m.
Paraonis, abranchiate, Hartman 1967 p. 111. Drake Passage and South Shetland Islands, 3867–4086 m.

SPIONIDAE, with 10 species in 5 genera

Laonice antarcticae Hartman. Northwest Atlantic Ocean, 1102–2846 m (Hartman and Fauchald 1971 USC).
Laonice cirrata (Sars). Northwest Atlantic Ocean, slope and abyssal depths (Hartman 1965 p. 148).
Paraprionospio pinnata (Ehlers). Velero basin, California, 2360 m (Hartman 1960 p. 270).
Polydora sp. Hartman and Fauchald 1971 USC. Northwest Atlantic Ocean, 196–3834 m.
Prionospio cirrifera Wiren. Northwest Atlantic Ocean, slope and abyssal depths to 2900 m (Hartman and Fauchald 1971 USC).
Prionospio steenstrupi Malmgren. Arctic Ocean and boreal Atlantic Ocean, 188–3361 m (Ditlevsen 1937 p. 57; and Hartman 1965 p. 152).
Prionospio spp. Northwest Atlantic Ocean, 196–5023 m (Hartman and Fauchald 1971 p. 105).
Spiophanes fimbriata Moore. Velero basin, California, 2115 m (Hartman 1960 p. 270).

Spiophanes kroeyeri Grube. Northwest Atlantic Ocean, 96–3828 m (Hartman 1965 p. 153; and Hartman and Fauchald 1971 p. 105).
Spiophanes sp. Mid-Pacific and Antarctic basin, 4675 m (Hartman 1965 p. 114).

MAGELONIDAE, with 2 species in 1 genus

Magelona capax Hartman 1965 p. 158. Midwestern Atlantic Ocean, 4769 m.
Magelona spp. Hartman 1965 p. 159. Northwest Atlantic Ocean, 3753–5000 m.

DISOMIDAE, with 1 species

Disoma watsoni Fauvel. Northwest Atlantic Ocean, in 530–3753 m (Hartman 1965 p. 159).

POECILOCHAETIDAE, with 4 species in 1 genus

Poecilochaetus bermudensis Hartman 1965 p. 160. Off Bermuda Islands, 2000 m.
Poecilochaetus fulgoris Ehlers. Northwest Atlantic Ocean, 650–5000 m (Hartman 1965 p. 162).
Poecilochaetus vitjazi Levenstein 1962 p. 1145. Tonga trench, 10,687–10,415 m.
Poecilochaetus sp. Northwest Atlantic Ocean, 2022–5023 m (Hartman and Fauchald 1971 p. 108).

HETEROSPIONIDAE, with 1 species

Heterospio longissima Ehlers. Northwest Atlantic Ocean, 1500–4950 m (Hartman 1965 p. 164).

CHAETOPTERIDAE, with 3 species in 3 genera

Phyllochaetopterus sp. Northwest Atlantic Ocean, slope depths to 4500 m (Hartman 1965 p. 164); Mozambique basin, see above.
Spiochaetopterus typicus Sars. Bering Sea, 113–3932 m (Levenstein 1961a p. 158).
?*Telepsavus* sp. Northwest Atlantic Ocean, 4892–4743 m (Hartman and Fauchald 1971 p. 109).

CIRRATULIDAE, with 12 species in 3 genera

Chaetozone benthaliana McIntosh 1885 p. 386. Off Halifax, N.S., 2275 m.
Chaetozone gayheadia Hartman 1965 p. 166. Northwest Atlantic Ocean, 530–2022 m.
Chaetozone gracilis (Moore 1923 p. 187). Off southern California, 4016 m.
Chaetozone setosa Malmgren. Northwest Atlantic Ocean, 97–4436 m (Hartman 1965 p. 167).
Chaetozone spp. Northwest and equatorial Atlantic Ocean, slope depths to 4825 m (Hartman 1965 p. 166); Mozambique basin (see above).
Cirratulus abyssorum Hansen 1878 p. 10. North Sea, abyssal. (Perhaps a species of *Chaetozone*.)
Cirratulus sp. Falkland Islands, 2452 m (Hartman 1967 p. 117).
Tharyx annulosus Hartman 1965 p. 169. Northwest Atlantic Ocean, 200–4950 m; Drake Passage and Scotia Sea, Antarctica, in 2366–3806 m (Hartman 1967 p. 118).
Tharyx marioni (St. Joseph). Off Santiago, Chile, and Drake Passage, 3651–3927 m (Hartman 1967 p. 118).
Tharyx multifilis Moore. Banda trench, 6580 m (Kirkegaard 1956 p. 70); Java trench, abyssal (Levenstein 1961b p. 136).
Tharyx nigrostrum Hartman and Fauchald 1971 p. 111. Northwest Atlantic Ocean, 1102–4825 m.
Tharyx spp. Hartman 1965 p. 170. Northwest Atlantic Ocean, 196–4825 m. Mozambique basin, see above.

COSSURIDAE, with 3 species in 1 genus

Cossura abyssalis Hartman 1967 p. 118. Off Valparaiso, Chile, 3655–3651 m.
Cossura candida Hartman. Velero basin, California, 2115 m (Hartman 1960 p. 270).
Cossura longicirrata Webster and Benedict. Java trench, abyssal (Levenstein 1961b p. 136); northwest Atlantic Ocean, 97–5023 m (Hartman 1965 p. 170).

CTENODRILIDAE, with 1 species

Zeppelina prolonga Hartman 1965 p. 172. Off New England, 1500–3752 m.

FLABELLIGERIDAE, with 13 species in 5 genera

Brada bransfieldia Hartman 1967 p. 120. South Shetland Islands, Antarctica, 311–4758 m.
**Bradabyssa papillata* Hartman 1967 p. 122. Scotia Sea, Antarctica, 2815–2818 m.
**Buskiella abyssorum* McIntosh 1885 p. 372. Off Sierra Leone, Africa, 311–4758 m.
**Ilyphagus bythincola* Chamberlin 1919 p. 402. Off western Mexico, 3436 m; Sunda trench, to 6740 m (Kirkegaard 1956 p. 70); Kurile-Kamchatka trench, abyssal (Levenstein 1961a p. 136).
Ilyphagus coronatus Monro. Eastern sector of Antarctica, 1437–3514 m (Hartman 1967 p. 127).
Ilyphagus gravieri (McIntosh). South of Australia, 3292 m (Hartman 1967 p. 127).
Ilyphagus hirsutus Monro 1937 p. 304. South Arabian Sea, 3385 m.
Ilyphagus irenaia (Chamberlin 1919 p. 400). Off Pacific Panama, 3280 m. Bering Sea, 1580–3330 m (Levenstein 1961a p. 159, as *Brada*).
Ilyphagus octobranchus Hartman 1965 p. 178. Northwest Atlantic Ocean, 300–4820 m.
Ilyphagus pluto Chamberlin 1919 p. 403. Off Peru, 5203 m.
Ilyphagus wyvillei (McIntosh 1885 p. 366). South of Australia, 3510 m. Bering Sea, 3550 m (Levenstein 1961a p. 160).
Ilyphagus sp. Hartman and Fauchald 1971 p. 121. Northwest Atlantic Ocean, 1330–4892 m. Mozambique basin, see above.
Pherusa sarsi (McIntosh 1922 p. 8). Antarctic Ocean, 3612 m (as *Trophonia*).

FAUVELIOPSIDAE, with 10 species in 4 genera

**Bruunilla natalensis* n.sp. Mozambique basin, see above.

**Fauveliopsis brevipodus*, new name for *F. brevis* Hartman 1967 p. 123. Shag Rocks and Drake Passage, Antarctica, 384–3537 m.

Fauveliopsis brevis (Hartman 1965 as *Brada*). Off New England, 1330–5007 m (Hartman and Fauchald 1971 USC).

Fauveliopsis challengeriae McIntosh 1922 p. 9. Between Australia and Antarctica, 3566 m.

Fauveliopsis glabra (Hartman 1960, as *Brada*). Off northwest Atlantic Ocean, 530–5023 m (Hartman 1965 p. 173).

Fauveliopsis scabra Hartman and Fauchald 1971 p. 117. Northwest and mid-Atlantic Ocean, 530–5023 m.

Fauveliopsis sp. Mozambique basin, see above.

**Flabelligella minuta* Hartman 1965 p. 37. Northwest Atlantic Ocean; Mozambique basin, see above.

Flabelligella papillata Hartman 1965 p. 177. Northwest Atlantic Ocean, 1135–4825 m.

Flota flabelligera Hartman 1967 p. 125. Off southwest Chile, pelagic over 4008–4100 m.

SCALIBREGMIDAE, with 12 species in 9 genera

Asclerocheilus beringianus Uschakov. Northwest Atlantic Ocean, 4833–5023 m (Hartman 1965 p. 181).

Asclerocheilus intermedius (St. Joseph). Northwest Atlantic Ocean, 1135–2886 m (Hartman and Fauchald 1971 p. 123).

**Neolipobranchius glabrus* Hartman and Fauchald 1971 p. 124. Northwest Atlantic Ocean, 4436 m.

**Proscalibregma linea* Hartman 1967 p. 132. Drake Passage, Antarctica, 3312–3532 m.

**Pseudoscalibregma aciculata* Hartman 1965 p. 182. Off New England, 2000–4892 m (Hartman and Fauchald 1971 USC).

Pseudoscalibregma pallens Levenstein 1962 p. 1146. Kermadec trench, 8928–9174 m.

Pseudoscalibregma parva (Hansen). Northwest Atlantic Ocean, 300–2900 m (Hartman 1965 p. 183); Bering Sea, 1793–3680 m (Levenstein 1961a p. 161, as *Pseudoscalibregma longisetosum*).

Pseudoscalibregma sp. Hartman and Fauchald 1971 p. 125. Northwest Atlantic Ocean, 2496 m.

Scalibregma inflata Rathke. Bering Sea, 28–4400 m (Levenstein 1961a p. 161); northwest Atlantic Ocean, 2886 m (Hartman 1965 p. 183); Mozambique basin, see above.

**Scalibregmella antennata* Hartman and Fauchald 1971 p. 126. Northwest Atlantic Ocean, 4825–5023 m.

**Scalispinigera cirrata* Hartman and Fauchald 1971 p. 128. Northwest Atlantic Ocean, 2022 m.

**Sclerobregma branchiata* Hartman 1965 p. 182. Northwest Atlantic Ocean, 400–2500 m (Hartman and Fauchald 1971 p. 129).

OPHELIIDAE, with 20 species in 6 genera

Ammotrypane abranchiata (Stop-Bowitz). Northwest Atlantic Ocean, 300–4500 m (Hartman 1965 p. 187).

Ammotrypane ?aulogaster Rathke. Northwest Atlantic Ocean, 4663 m (Hartman and Fauchald 1971 p. 129).

Ammotrypane aulogastrella Hartman and Fauchald 1971 p. 130. Northwest and mid-Atlantic Ocean, 196–5023 m.

Ammotrypane brevibranchiata Caullery. Mozambique basin, see above.

Ammotrypane chaetifera Hartman 1965 p. 188. Northwest Atlantic Ocean, 1330–5007 m.

Ammotrypane cylindricaudatus Hansen. Northwest Atlantic Ocean, 530–2862 m (Hartman and Fauchald 1971 p. 131).

Ammotrypane galathae Kirkegaard 1956 p. 71. Banda trench, 7250–7290 m.

Ammotrypane nematoides Ehlers. Drake Passage and South Shetland Islands, 2763–4758 m (Hartman 1967 p. 137).

Ammotrypane nybelini Eliason 1951 p. 135. North Atlantic Ocean, 4540–4600 m.

**Ammotrypanella arctica* McIntosh. North Atlantic Ocean, 3264–4360 m (Hartman and Fauchald 1971 p. 132); Off Azores, 4360 m (Fauvel 1914 p. 246).

Euzonus (*Thoracophelia*) *profundus* Hartman 1967 p. 137. Off Cape Horn, 4008 m.

**Kesun abyssorum* Monro. Sunda and Kermadec trenches, 6960–8300 m (Kirkegaard 1956 p. 71); Kurile trench, abyssal (Levenstein 1961b p. 136); Antarctic basin, to 4685 m (Hartman 1967 p. 138).

Kesun fusus Chamberlin 1919 p. 386. Marquesas Islands, 4504 m.

Kesun gravieri (McIntosh). North and mid-Atlantic Ocean, 780–4833 m (Hartman 1965 p. 191, as *Travisia*).

Kesun glandulosa (McIntosh 1879 p. 506, as *Travisia*). Davis Strait, Greenland, 3264 m.

Kesun nigrocincta (Ehlers 1913 p. 525, as *Travisia*). Eastern Antarctic Ocean, 2725 m.

**Tachytrypane jeffreysii* McIntosh. Gulf of Gascony, 3910 m (Fauvel 1914 p. 249); northwest Atlantic Ocean, 2496–4859 m (Hartman 1965 p. 190).

Travisia antarctica Hartman 1967 p. 139. South Georgia and South Shetland Islands, Antarctica, 2452–2727 m.

Travisia profundi Chamberlin 1919 p. 387. Off Peru, 4063 m; Banda trench, 6490–6650 m (Kirkegaard 1956 p. 70); south Pacific basin, 4789–4795 m (Hartman 1967 p. 162).

Travisia pupa Moore. Bering Sea, 1740–2416 m (Levenstein 1961a p. 162).

STERNASPIDAE, with 2 species in 1 genus

Sternaspis scutata Ranzani. Bering Sea, 4400–4418 m (Levenstein 1961*a* p. 167).

Sternaspis sp. Northwest Atlantic Ocean, 2862–3891 m (Hartman and Fauchald 1971 p. 135).

CAPITELLIDAE, with 11 species in 6 genera

Barantolla, near *americana* Hartman. Northwest Atlantic Ocean, 2000–3753 m (Hartman and Fauchald 1971 p. 135).

Capitella aberranta Hartman and Fauchald 1971 p. 136. Northwest Atlantic Ocean, 4862 m.

Capitella, near *capitata* (Fabricius). Northwest Atlantic Ocean, 2000–4825 m (Hartman and Fauchald 1971 p. 136).

Dasybranchus sp. Northwest Atlantic Ocean, 3753 m (Hartman and Fauchald 1971 p. 137).

Heteromastus filiformis (Claparede). Northwest Atlantic Ocean, 97–4680 m (Hartman 1965 p. 193).

Leiochrides hemipodus Hartman. Velero basin, California, 2115 m (Hartman 1960 p. 270).

?*Leiochrides* sp. Northwest Atlantic Ocean, 3806 m (Hartman and Fauchald 1971 p. 138).

Notomastus agassizii McIntosh 1885 p. 389. Off New York, 2439 m.

Notomastus latericeus Sars. Northwest Atlantic Ocean, 200–4360 m (Hartman 1965 p. 194); northeast Atlantic Ocean, 4360 m (Fauvel 1914 p. 250); Bering Sea, 37–4000 m (Levenstein 1961a p. 162).

Notomastus teres Hartman 1965 p. 194. Northwest Atlantic Ocean, 467–2891 m (Hartman and Fauchald 1971 p. 139).

Notomastus sp. Kermadec trench, 8210–8300 m (Kirkegaard 1956 p. 72); Java trench, abyssal (Levenstein 1961b p. 136). Velero basin, California, 2360 m (Hartman 1960 p. 270).

MALDANIDAE, with 36 species in 17 genera

**Abyssoclymene annularis* Hartman 1967 p. 143. Circum-Antarctic Ocean, 2196–5051 m.

Asychis amphiglypta abyssicola Elisaon 1951 p. 136. Mid-Atlantic Ocean, 5033–5044 m.

Asychis ramosus Levenstein 1961a p. 165. Bering Sea, 2416–3940 m.

?*Axiothella* sp. Northwest Atlantic Ocean, 2500 m (Hartman 1965 p. 200).

Clymenura borealis (Arwidsson). Northwest Atlantic Ocean, 400–4892 m (Hartman 1965 p. 200).

Clymenura sp. Northwest and mid-Atlantic Ocean, 4825–4850 m (Hartman and Fauchald 1971 p. 140).

Isocirrus planiceps (Sars). Northwest Atlantic Ocean, 4663–4970 m (Hartman and Fauchald 1971 p. 140).

Isocirrus sp. Northwest Atlantic Ocean, 4750–5000 m (Hartman and Fauchald 1971 p. 141).

Lumbriclymene nasutus Wesenberg-Lund. Northwest Atlantic Ocean, 2900 m (Hartman 1965 p. 202).

**Lumbriclymenella robusta* Arwidsson. South Georgia and Scotia Sea, 2818–2815 m (Hartman 1965 p. 145).

Maldane malmgreni McIntosh 1885 p. 393. Off Strait of Gibraltar, 2775 m.

Maldane sarsi Malmgren. Banda Sea, 4391 m (Mesnil and Fauvel 1939 p. 14); Bering Sea, 66–3680 m (Levenstein 1961b p. 164); northwest Atlantic Ocean, 97–4437 m (Hartman 1965 p. 204).

**Maldanella antarctica* McIntosh 1885 p. 394. Antarctic Ocean, 2502 m.

Maldanella davisi Wesenberg-Lund 1948 p. 35. Davis Strait, Greenland, 3229 m.

Maldanella fibrillata Chamberlin 1919 p. 413. Pacific Panama, 3436 m.

Maldanella harai (Izuka). North Atlantic Ocean, 4380 m (Fauvel 1914 p. 261); Kermadec trench, 6620–6720 m (Kirkegaard 1956 p. 72); Java trench, abyssal (Levenstein 1961a p. 164).

Maldanella neozealaniae McIntosh 1885 p. 398. Queen Charlotte Sound, New Zealand, 1100 fath.

Maldanella valparaisiensis McIntosh 1885 p. 396. Off Chile, 4070 m.

Microclymene tricirrata Arwidsson. Bering Sea, 4400–3520 m (Levenstein 1961b p. 163).

Nicomache ?*benthaliana* McIntosh 1885 p. 400. Off Japan, 4206 m.

Nicomache lumbricalis (Fabricius). Northwest Atlantic Ocean, 500–4997 m (Hartman 1965 p. 204).

Nicomache sp. Mozambique basin, see above.

Notoproctus abyssus Hartman and Fauchald 1971 p. 142. Northwest Atlantic Ocean, 1330–3806 m.

Notroproctus oculatus Arwidsson, Bering Sea, 2440–2770 m (Levenstein 1961a p. 163).

Notoproctus oculatus, anoculate, Hartman 1965 p. 205. Northwest Atlantic Ocean, 2000–2886 m.

Notoproctus oculatus antarcticus Arwidsson. Antarctic Ocean, 3397 m (Ehlers 1913 p. 547).

Notoproctus pacificus, sensu Mesnil and Fauvel 1939 p. 9. Banda trench, 4016–4391 m.

Notoproctus scutiferus Wesenberg-Lund 1948 p. 19. West of Greenland, 3229 m.

?*Petaloproctus cirratus* Monro. Banda trench, 7250–7290 m (Kirkegaard 1956 p. 73).

Petaloproctus tenuis (Theel). Bering Sea, 3100–4400 m (Levenstein 1961a p. 163).

Praxilla occidentalis McIntosh 1885 p. 407. Off New York, N.Y., 2257 m.

Praxillella abyssorum (McIntosh 1885 p. 408). Antarctica, 3566 m.

Praxillella gracilis (Sars). Northwest Atlantic Ocean, 1102–2478 m (Hartman 1965 p. 206).

Praxillella praetermissa (Malmgren). Northwest Atlantic Ocean, 2000–4950 m (Hartman 1965 p. 206).

Rhodine sp. Northwest Atlantic Ocean, 3753–4768 m (Hartman 1965 p. 207).

**Sonatsa meridionalis* Chamberlin 1919 p. 416. Off Peru, 4063 m.

OWENIIDAE, with 5 species in 2 genera

Myriochele pacifica McIntosh 1885 p. 413. Mid-Pacific basin, 4755 m.

Myriochele, near *heeri* Malmgren. Northwest Atlantic Ocean, 1102–4680 m (Hartman and Fauchald 1971 p. 146).

Myriochele spp. Kermadec trench, 8210–8300 m (Kirkegaard 1956 p. 73); northwest Atlantic Ocean, 2000–5023 m (Hartman and Fauchald 1971 p. 147); Mozambique basin (see above).

?*Owenia fusiformis* delle Chiaje. Banda Sea, 4391 m (Mesnil and Fauvel 1939 p. 22); North Atlantic Ocean, 4554 m (Hartman 1965 p. 210).
?*Owenia lobopygidiata* Uschakov. Banda trench, 3762–3936 m (Kirkegaard 1956 p. 73).

BOGUEIDAE, with 1 species

**Boguella ornata* Hartman and Fauchald 1971 p. 149. Off Bermuda Islands, 2095–2222 m.

SABELLARIIDAE, with 3 species in 2 genera

**Monorchos* sp. Northwest Atlantic Ocean, 4806 m (Hartman and Fauchald 1971 p. 151); Mozambique basin, see above.
**Phalacrostemma cidariophilum* Marenzeller. Off Bermuda Islands, 2095–2223 m (Hartman and Fauchald 1971 p. 151).
Phalacrostemma elegans Fauvel. Northwest Atlantic Ocean, 770–5007 m (Hartman and Fauchald 1971 p. 152); Mozambique basin, see above).

PECTINARIIDAE, with 1 species

Petta assimilis McIntosh 1885 p. 423. Off Kerguelen Islands, 2192 m. Off Cape Horn and Falkland Islands, 1806–2452 m (Hartman 1967 p. 152).

AMPHARETIDAE, with 54 species in 30 genera

Amage asiaticus Uschakov 1955b p. 378. Bering Sea, 28–2900 m.
Amage sculpta Ehlers. Drake Passage, Antarctica, 2672–3030 m (Hartman 1967 p. 152).
Amage sp. Northwest Atlantic Ocean, 196–5042 m (Hartman and Fauchald 1971 p. 153).
**Amelinna abyssalis* Hartman 1969 p. 533. San Clemente basin, California, abyssal depths.
Amelinna armipotens (Moore 1923 p. 215). Off southern California, 4075 m, as *Sosanopsis*. (Hartman 1969 p. 535).
**Ampharana antarctica* Hartman 1967 p. 154. Mid-Pacific-Antarctic basin, 4813 m.
Ampharete arctica Malmgren. North Atlantic Ocean, 97–4680 m (Hartman 1965 p. 213).
Ampharete kerguelensis McIntosh. South Georgia and Antarctic Ocean, 128–2727 m (Hartman 1967 p. 154).
Amphicteis gunneri (Sars). Northwest Atlantic Ocean, 2802–2891 m (Hartman 1965 p. 213).
Amphicteis gunneri atlantica McIntosh 1885 p. 429. Mid-Atlantic Ocean, 5030 m.
Amphicteis gunneri japonica McIntosh. Bering Sea, 79–3330 m (Levenstein 1961a p. 170).
Amphicteis mederi Annenkova. Kurile-Kamchatka trench (Uschakov 1952 p. 110).
Amphicteis sargassoensis Hartman and Fauchald 1971 p. 154. North and mid-Atlantic Ocean, 3806–5023 m.
Amphicteis sarsi McIntosh 1885 p. 429. Off Buenos Aires, Argentina, 4846 m.
Amphicteis sibogae Caullery 1944 p. 82. Off East Indies, 2796 m.
Amphicteis trichophora Hartman and Fauchald 1971 p. 155. Northwest and equatorial Atlantic Ocean, 196–2886 m.
Amphicteis vestis Hartman 1965 p. 216. Northwest Atlantic Ocean, 200–2468 m.
Amphicteis wyvillei McIntosh 1885 p. 430. Off Kerguelen Islands, 2912 m.
**Anobothrella antarctica* (Monro). Antarctic Ocean, 298–4099 m (Hartman 1967 p. 156).
Anobothrus near *gracilis* Malmgren. Kurile-Kamchatka trench (Uschakov 1952 p. 110).
Anobothrus sp. Mozambique basin, see above.
**Eusamytha pacifica* McIntosh 1885 p. 436. Off Japan, 4026 m.
**Eusamythella*, new name, *sexdentata* (Hartman 1967 p. 157). (To replace *Eusamytha* Hartman 1967, not McIntosh 1885). Bransfield Strait, Antarctica, 2119–2562 m.
**Glyphanostomum abyssale* Day 1967 p. 703. Off Cape Town, South Africa, 2269 m.
Glyphanostomum pallescens (Theel). Bering Sea, 3100–3830 m (Levenstein 1961a p. 168). Arctic and Antarctic oceans, 298–4009 m (Hartman 1967 p. 158).
**Grubianella antarctica* McIntosh 1885 p. 432. Antarctica, eastern sector, 3595 m.
Lysippe annectens Moore. Velero basin, California, 2115 m (Hartman 1960 p. 270).
**Melinantipoda antarctica* Hartman 1967 p. 159. Antarctic–Pacific basin, 3848–4795 m.
Melinna armandi McIntosh 1885 p. 439. Off North Island, New Zealand, 2000 m.
Melinna buskii McIntosh 1922 p. 9. Australian Antarctic Ocean, 3566 m.
Melinna cristata (Sars). Bering Sea, 125–3680 m (Levenstein 1961a p. 167); Antarctic Ocean, 220–3803 m (Hartman, 1965, p. 160).
Melinna ochotica Uschakov. Okhotsk and Bering seas, 2440 m (Levenstein 1961a p. 167).
Melinna pacifica McIntosh 1885 p. 440. Mid-Pacific Ocean, 3750 m.
**Melinnampharete eoa* Annenkova. Bering Sea, 2995–4400 m (Levenstein 1961a p. 168).
**Melinnata americana* Hartman 1965 p. 219. Northwest Atlantic Ocean, 2000–4862 m.
**Melinnexis annenkovae* Uschakov 1952 p. 110. Northwest Pacific Ocean, abyssal depths.
Melinnexis collaris Hartman 1967 p. 161. Antarctic-Pacific basin, 4041–4813 m.
Melinnexis moorei Hartman 1960 p. 159. West of Santa Catalina Island, California, 1350–2182 fath.
Melinnexis rostrata (Wesenberg-Lund 1950a p. 49, as *Melinnides*). West off Greenland, 3229 m.
Melinnexis tentacula (Treadwell 1906 p. 1177 as *Terebellides*). Off Hawaiian Islands, 4126 m.
**Melinnopsis atlantica* McIntosh 1885 p. 441. Off Maryland, 3110 m and 4540–4600 m (Eliason 1951 p. 143).
**Moyanus explorans* Chamberlin 1919 p. 452. Off Peru, 4063 m.
**Neopaiwa cirrata* Hartman and Fauchald 1971 p. 159. Northwest Atlantic Ocean, under Sargasso Sea, 5007 m.

Neosabellides elongatus (Ehlers). Antarctic Ocean, 73–4758 m (Hartman 1967 p. 161).
**Neosamytha gracilis* Hartman 1967 p. 162. South Georgia, Antarctic region, 2663–2727 m.
**Pabits derodorus* Chamberlin 1919 p. 457. Marquesas Islands, South Pacific Ocean, 4504 m.
**Paiwa abyssi* Chamberlin 1919 p. 459. Off Peru, 4087 m.
**Phyllampharete longicirra* Hartman and Fauchald 1971 p. 161. Under Sargasso Sea, Atlantic Ocean, 5018–5023 m.
Samytha sexcirrata (Sars). Bering Sea, 4820 m (Levenstein 1961b p. 169).
Samythella bathycola Uschakov. Bering Sea, 3680 m (Levenstein 1961a p. 169).
Samythella elongata Verrill 1873 p. 99. Northwest Atlantic Ocean, 2022 m.
**Samythopsis grubei* McIntosh 1885 p. 435. Off Chile, 4070 m.
Sosane procera malayensis Caullery 1944 p. 85. Off Malay Archipelago, 2000–2794 m.
**Weddellia profundi* Hartman 1967 p. 164. South Sandwich trench, Antarctic Ocean, 2553–2575 m.

TEREBELLIDAE, with 27 species in 16 genera

Amaeana trilobata (Sars). Northwest Atlantic Ocean, 2891 m (Hartman and Fauchald 1971 p. 169).
Artacama proboscidea Malmgren. Bering Sea, 65–3330 m (Levenstein 1961a p. 171).
Axionice maculata (Dalyell). Arctic and North Atlantic oceans, in 19–2550 m (Ditlevsen 1937 p. 59, as *Scione lobata*).
Axionice spinifera (Ehlers). Antarctic Ocean, 223–4758 m (Hartman 1967 p. 169 as *Pista*).
**Bathya abyssorum* (McIntosh 1885 p. 461). Mid-Pacific Ocean, 5715 m.
Bathya neozealaniae (McIntosh 1885 p. 460). Off New Zealand, 2000 m.
**Ehlersiella atlantica* McIntosh 1885 p. 475. Off Azores, 5030 m.
**Eupistella darwini* (McIntosh 1885 p. 458, as *Eupista*). Off Chile, 5030 m.
Eupistella dibranchiata (Fauvel). North Atlantic Ocean, 5270 m (Fauvel 1914 p. 303).
Eupistella grubei (McIntosh 1885 p. 459, as *Eupista*). South Atlantic Ocean, 4846 m.
**Euthelepus abranchiatus* Hartman and Fauchald 1971 p. 171. Northwest Atlantic Ocean, 2022 m.
Euthelepus chilensis McIntosh 1885 p. 457. Off Chile, 3950 m.
Hauchiella sp. Off Antarctic Peninsula, 4310–4328 m (Hartman 1967 p. 116).
Lanassa benthaliana McIntosh 1885 p. 464. Mid-Atlantic Ocean, 5030 m.
Laphania boecki Malmgren. Northwest Atlantic Ocean, 2000–4667 m (Hartman 1965 p. 224).
**Leaena antarctica* McIntosh 1885 p. 462. Antarctic Ocean, 3612 m.
Leaena langerhansi McIntosh 1885 p. 462. Antarctic Ocean, 3335 m.
Leaena minima Hartman 1965 p. 225, as *Leaena collaris minima*. Off New England, 1000–2469 m.
Pista abyssicola McIntosh 1885 p. 453. Between Australia and Antarctica, 3566 m.
Pista brevibranchia Caullery 1944 p. 152. North of Sumbawa, East Indies, 2060 m.
Pista cristata (Mueller). Bering Sea, 105–3940 m (Levenstein 1961b p. 171).
Pista incarrientis Annenkova. Bering Sea, 2995–3713 m (Levenstein 1961a p. 171).
Pista mirabilis McIntosh. South Shetland Islands, Antarctica, 1437–2818 m (Hartman 1967 p. 169).
Streblosoma bairdi (Malmgren). Bering Sea, 2200 m (Levenstein 1961a p. 172).
**Stschapovella tatjanae* Levenstein 1957 p. 288. Bering Sea, 3100 m.
Thelepides koehleri Gravier. Drake Passage, Antarctica, 2672–3020 m (Hartman 1967 p. 171).
Thelepus cincinnatus (Fabricius). Bering Sea, 38–3940 m (Levenstein 1961 p. 172); Antarctic Ocean, 73–3239 m (Hartman 1967 p. 171).

TRICHOBRANCHIDAE, with 7 species in 4 genera

**Ampharetides vanhoeffeni* Ehlers 1913 p. 568. Eastern sector of Antarctica, 2725 m.
Terebellides eurystethus Chamberlin 1919 p. 438. Between Peru and Galapagos Islands, in 2600 fath. Kermadec trench, 6660–6720 m (Kirkegaard 1956 p. 74).
Terebellides intoshi Caullery 1944 p. 185. Off East Indies, 2700 m.
Terebellides lobatus Hartman and Fauchald 1971 p. 175. Northwest Atlantic Ocean, 1330–5007 m.
Terebellides stroemii Sars. Off Greenland, 9–2017 m (Ditlevsen 1937 p. 59); Bering Sea, 17–3908 m (Levenstein 1961a p. 170); northwest Atlantic Ocean, 196–2802 m (Hartman and Fauchald 1971 p. 177).
Trichobranchus glacialis Malmgren. Arctic Ocean, 120–2730 m (Ditlevsen 1937 59).
**Unobranchus abyssalis* Hartman 1965 p. 230. Northwest Atlantic Ocean, 4800–5023 m (Hartman and Fauchald 1971 p. 178).

SABELLIDAE, with 12 species in 5 genera

Chone infundibuliformis Kroeyer. Off Greenland, 3521 m (Wesenberg-Lund 1950a p. 131).
Euchone incolor Hartman 1965 p. 232. Northwest Atlantic Ocean, 196–4892 m.
Jasmineira filatovae Levenstein 1961a p. 173. Bering Sea, 3940 m.
Jasmineira schaudinni Augener 1912 p. 185. Off Spitsbergen, abyssal.
Jasmineira sp. Kermadec trench, 6620–8300 m (Kirkegaard 1956 p. 74); northwest Atlantic Ocean, 4743–4892 m (Hartman and Fauchald 1971 p. 180).
**Potamethus dubius* (Eliason 1951 p. 139, as *Potamis*). North Atlantic Ocean, 5850–5860 m.
Potamethus mucronatus (Moore 1923 p. 243, as *Notaulax*). Off southern California, 4016–4131 m.
Potamethus scotiae (Pixell 1913 p. 356, as *Potamis*). Eastern sector of Antarctica, 1410 fath.
Potamethus singularis Hartman 1965 p. 234. Northwestern Atlantic Ocean, 196–6023 m.

Potamethus spathiferus (Ehlers 1887 p. 278, as *Potamis*). North Atlantic Ocean, 4360 m (Fauvel 1914 p. 31).
?*Potamethus* sp. Mozambique basin, see above.
Potamilla abyssicola Uschakov 1952 p. 111. North Pacific Ocean, 4100–4200 m.

SERPULIDAE, with 12 species in 10 genera

Apomatus similis Marion and Bobretzky. Off Azores, North Atlantic Ocean, 4100 m (Fauvel 1914 p. 359).
Ditrupa arietina (Mueller). West of Greenland, 2730 m (Ditlevsen 1937 p. 59).
Ditrupa groenlandica McIntosh 1879 p. 509. Davis Strait, Greenland, 1450 fath.
?*Filogranula* sp. Hartman and Fauchald 1971 p. 182. Northwest Atlantic Ocean, 3834–4892 m.
Hydroides norvegica (Gunnerus). Gulf of Gascony, France, 4808 m (Fauvel 1914 p. 324).
Placostegus benthalianus McIntosh 1885 p. 524. Mid-Pacific Ocean, 5715 m.
Placostegus moerchii McIntosh 1885 p. 524. South Pacific Ocean, 4343 m.
Placostegus ornatus (Moerch). Mid-Pacific and Atlantic oceans, 2900 fath (McIntosh 1885 p. 522).
Pomatoceros triqueter (Linnaeus). Gulf of Gascony, France, 4808 m (Fauvel 1914 p. 348).
Protis arctica (Hansen). North and mid-Atlantic Ocean, 5250–5300 m (Eliason 1951 p. 142).
?*Serpula* sp. Mozambique basin, see above.
Spirobranchus jousseaumei Gravier). Banda Sea, 4892 m (Mesnil and Fauvel 1939 p. 34).
Vermiliopsis langerhansi Fauvel 1914 p. 344. Off Azores, 4020 m.

MYZOSTOMIDAE, with 3 species in 2 genera

Myzostomum cysticolum von Graff. South Sandwich Islands, 4643–4645 m (Hartman 1967 p. 102).
Myzostomum compressum von Graff 1884 p. 42. Off Crozet Islands, Antarctica, 2516 m.
Stelechopus hydrocrini von Graff 1884 p. 76. Crozet Islands, Antarctica, 1375 fath.

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A New Polychaete Species of the Genus *Macellicephaloides* from the Aleutian Trench

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Levenstein, R. Y. 1971. A new polychaete species of the genus *Macellicephaloides* from the Aleutian Trench. J. Fish. Res. Bd. Canada 28: 1429–1431.

A new species of polychaete, *Macellicephaloides berkeleyi*, is described. The description is based on two specimens collected at a depth of 7000 m from the Aleutian Trench. The species is thought to be an intermediate link between the genera *Macellicephala* and *Macellicephaloides*.

Levenstein, R. Y. 1971. A new polychaete species of the genus *Macellicephaloides* from the Aleutian Trench. J. Fish. Res. Bd. Canada 28: 1429–1431.

On décrit une nouvelle espèce de polychète, *Macellicephaloides berkeleyi*. Cette description repose sur deux spécimens recueillis à une profondeur de 7000 m dans la fosse des Aléoutiennes. Il se peut que l'espèce soit le trait d'union entre les genres *Macellicephala* et *Macellicephaloides*.

Received March 17, 1971

Voluminous material on different benthic groups, including Polychaeta, was collected during the 45th cruise of the R/V *Vityaz* (1969), which covered the area of the Gulf of Alaska and the Aleutian Trench. The interesting polychaetous collections from the Aleutian Trench contained a representative of the genus *Macellicephaloides* Uschakov 1955. This genus is one of the rarest among polychaetes and bottom invertebrates, and can be considered an endemic representative of the oceanic hadal zone. So far, species of this genus have been known to exist in Kurile-Kamchatka, Japan, and Mariana trenches (Uschakov 1955; Levenstein 1962, 1971). In the Aleutian Trench a representative of this species was found for the first time. The new species has been called *Macellicephaloides berkeleyi* in honour of Dr Cyril Berkeley, who is one of the well-known specialists on polychaetes.

Macellicephaloides berkeleyi n.sp.

(Fig. 1)

Material Examined

Station 6085 (50°48′6N, 173°29′W): depth 7000 m; character of the bottom — clay mud; Sigsbee trawl; 2 specimens, body length 30 and 28 mm, width with parapodia 12 and 10 mm respectively. Proboscis 10 × 5 mm.

Description

Body consists of 25 or 26 segments including the first palpal segment. Prostomium conical, prostomial peaks absent. Lacks eyes. Median antenna reduced, its base low, hardly visible. Palpi thin and long. Tentacular cirri unequally long, upper one somewhat shorter than the palp, lower one almost twice as long as the latter. No setae found at base of tentacular cirri.

Proboscis large, ⅓ of the body length. Two cirriform appendages at distal end of proboscis, 8 soft transparent vesicular papillae on ventral and dorsal borders of the proboscis. Two opposing pair of inner chitinous teeth (Fig. 1*a*).

Elytra lost, elytral scars large, numbering 9 pair. Dorsal tentacular cirri have a low cylindrical cirrophore with a very long cirrostyle, much longer than the parapodium. No dorsal tubercles on cirrigerous segments (Fig. 1*b*). Notopodium reduced, represented by tuft of setae and an aciculum. Notosetae thin with long pointed ends, with two lateral rows of denticles (Fig. 1*c*).

Neuropodium massive, circular, ending with an elongated tip bearing the aciculum. Lateral lips hardly visible. Ventral cirri medium length, except cirrus on second setal segment, which is longer than the parapodium. Neurosetae more numerous and larger than notosetae. Body pale colored (Fig. 1*d*).

Conclusions

The described specimens belong undoubtedly to the genus *Macellicephaloides* because the dis-

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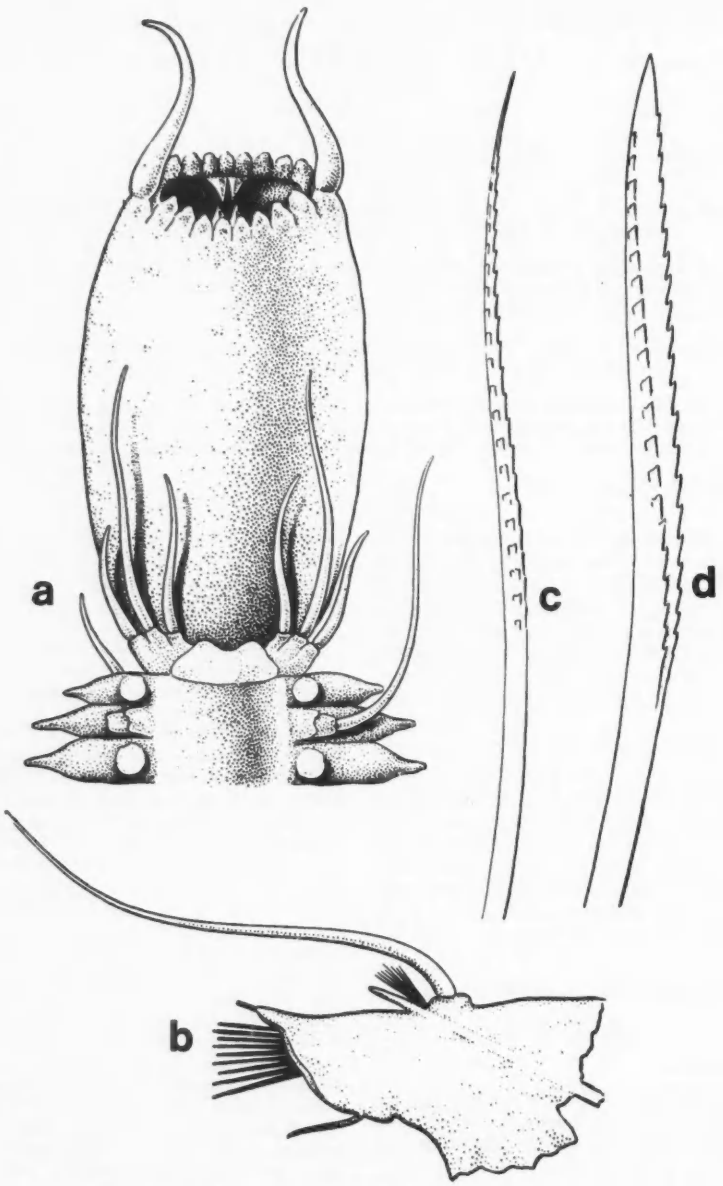

FIG. 1. *Macellicephaloides berkeleyi* n.sp. *a*, Anterior body from the dorsal side with an everted pharynx; *b*, parapodium from a median segment; *c*, notoseta; *d*, neuroseta.

tinguishing feature of the latter is the presence of two long lateral cirriform appendages at the anterior border of the proboscis. However, the specimens differ considerably from the earlier described species of this genus and possess a number of features likening them to *Macellicephala*. Our species is characterized by notosetae resembling setae of *Macellicephala*, the lack of large acicular setae poorly pronounced lateral lips of neuropodium, a low base of the median antenna, and a number of other features characteristic of *Macellicephala*. The described species is evidently a connecting link between *Macellicephala* and *Macellicephaloides*.

DISTRIBUTION

Aleutian Trench, depth 7000 m.

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Relation Between Tube-Building and Feeding in *Neoamphitrite robusta* (Polychaeta: Terebellidae)[1]

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Brown, P. L., and D. V. Ellis. 1971. Relation between tube-building and feeding in *Neoamphitrite robusta* (Polychaeta: Terebellidae). J. Fish. Res. Bd. Canada 28: 1433–1435.

Tube-building and feeding behaviour of *Neoamphitrite robusta* shared similar initial activities of tentacle extension, particle gathering, and passage of particles to the oral region. Particles were sorted by the inner lips, but the extent of sorting depended upon whether the animal was tube-building or feeding. Particles to be incorporated into the tube were passed over the outer lips and moulded into the tube in a stereotyped manner. Tube-rebuilding in test specimens (tubes removed) proceeded significantly faster than tube-building in control specimens (within tubes), although feeding was significantly less in the test specimens. Nonfeeding specimens were able to construct tubes. The two behaviours were able to proceed independently, although feeding supplemented tube-building with the passage of rejected particles to the tube.

Brown, P. L., and D. V. Ellis. 1971. Relation between tube-building and feeding in *Neoamphitrite robusta* (Polychaeta: Terebellidae). J. Fish. Res. Bd. Canada 28: 1433–1435.

La construction du tube et l'alimentation de *Neoamphitrite robusta* comportent initialement la même séquence: extension des tentacules, collection des particules, et leur transport vers la région buccale. Les particules sont triées par les lèvres internes, mais le degré de triage diffère suivant que l'animal construit son tube ou se nourrit. Les particules destinées au tube sont passées par-dessus les lèvres externes et façonnées dans le tube d'une façon stéréotypée. Les sujets expérimentaux (tubes enlevés) reconstruisent leur tube nettement plus vite, mais se nourrissent à un degré appréciablement moindre que les sujets témoins (tubes intacts). Les spécimens qui ne se nourrissent pas sont quand même capables de construire leur tube. Les deux opérations peuvent s'effectuer séparément, bien que l'alimentation contribue à la construction du tube par le transfert vers le tube des particules rejetées.

Received April 7, 1971

Neoamphitrite robusta feeds on, and builds its tube from, particles gathered from the sediments that it inhabits. The tube may be the product of activity specific for tube-building, as has been shown for a few other polychaetes (e.g., Barnes 1965), but could also be the result of the worm rejecting particles unsuitable for feeding and disposing of them in a functional manner. The former pattern would appear to have more survival potential than the latter. The hypothesis that tube-building is a distinct behaviour with a causal mechanism independent of that resulting in feeding is tested here.

Materials and Methods

All specimens were collected, just prior to experiments, from under floats at Oak Bay marina, Victoria, B.C. Their tubes consisted of fine sediment particles with additions of broken shell, plant pieces, portions of other tubes, and carcasses of other organisms, such as Crustacea. Stomachs contained very fine green organic matter including unidentified diatoms. Preliminary laboratory experiments showed that tubes were readily constructed from mud, noncombusted and combusted (sterile) sand, broken shell, plant debris, and brine shrimp eggs (edible).

Test specimens were removed from their tubes, whereas controls were left undisturbed. Tests and controls were placed in separate petri dishes containing aerated, cooled, sea water, and sufficient particles of either brine shrimp eggs or combusted sand for rebuilding a complete tube.

[1]Based on a thesis submitted by P.L.B. in partial fulfilment of the requirements for the degree of Bachelor of Science (Honours Zoology) from the University of Victoria.

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Behavioural observations were made on the method of tube-rebuilding. Rates of tube construction were measured by means of a grid under the petri dishes and consumption of particles was determined by stomach analyses.

Results

Test worms removed from tubes extended their tentacles to gather particles. These were transported first to the oral region by ciliary and muscular action as for *Amphitrite johnstoni* (Dales 1955), then down the ciliated upper lip to the outer lip pair, where they were taken into the inner lips. They were then rejected and propelled onto the ventral shield. Continual movement of particles from the mouth created a long string, which adhered to a mucouslike envelope secreted by the worm (Fig. 1A). Rotations of the worm, plus body wall pulsations and rowing motions of the parapodial setae, wrapped the string around the body to form a collar (Fig. 1B). By distending the body anteriorly and pressing on to the edge of the continuously growing collar, it was compacted and the characteristic long cylindrical tube was rebuilt. Completion of tube-rebuilding is defined as construction of a tube long enough to cover the worm. This usually occurred in less than a day. Subsequent tube-building involved a similar method of construction.

There was an observable but unquantifiable behavioural difference between tests and controls in that test specimens responded faster and more vigorously in extending tentacles and gathering particles until tube-rebuilding was complete.

Tests using edible particles (brine shrimp eggs) showed that tube-rebuilding by test specimens proceeded faster than tube-building by controls for periods up to 16 hr (Table 1). By 7 days (tube-rebuilding completed) building rates were not significantly different. Control specimens initially ingested significantly more organic particles, but by 7 days this feeding difference had disappeared (Table 2). It was also noticed that tube-building proceeded significantly ($P < 0.001$) faster at night ($\bar{x}$ 0.51 ± .04 cm/hr) than during the day ($\bar{x}$ 0.03 ± .02 cm/hr).

Repeat of the tests providing sterile sand or brine shrimp eggs to five test specimens each resulted in no feeding on sand, but feeding on brine shrimp eggs to a mean value of 60 eggs after 4 hr. Both sets of test specimens rebuilt tubes. After testing, it was found that some nonfeeding specimens (tests and controls) were gravid, with sunken stomachs, and were presumably unable to feed. Tube-building rates of such specimens were not significantly different from those of feeding specimens.

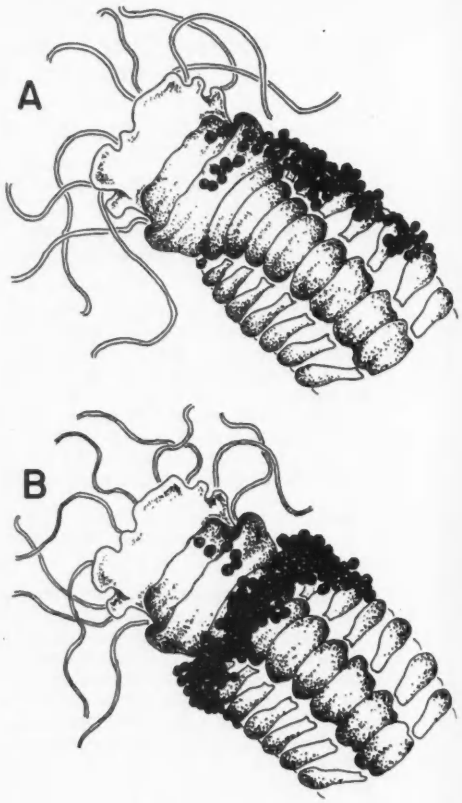

FIG. 1. Tube-rebuilding. Anterior portion of worm showing lip and ventral shield regions. (A) Particles moving from the mouth form a long string adhering to the side of the worm; (B) movements of the worm wrap the string around the body to form a collar, the beginning of a new tube.

TABLE 1. Mean tube-building rate (cm/hr) of test and control specimens. Each mean calculated from five individuals.

Time after expt began (*hr*)	Test specimens	Controls	*P*
2	1.45	0.35	<0.001**
5	0.92	0.28	<0.025**
16	0.36	0.14	<0.025**
7 days	0.12	0.08	>0.10*

** **Significant difference; *no significant difference.

TABLE 2. Mean numbers of brine shrimp eggs found in worm stomachs. Each mean calculated from five individuals with exception of the 2-hr test in which results from one extremely actively feeding test individual (750 eggs) have been removed from the data.

Time after expt began (*hr*)	Test specimens	Controls	*P*
2	0.25	46.25	<0.05** [a]
5	6.60	225.60	<0.05**
16	9.00	994.00	<0.05**
7 days	18.20	30.20	>0.05*

[a] **Significant difference; *no significant difference.

Conclusions

Tube-rebuilding, tube-building, and feeding behaviour under test conditions showed similar initial activities of tentacle extension, particle gathering, and passage of particles to the oral region, where sorting between the inner lips determined destination of particles. Under test conditions, tube-rebuilding proceeded significantly faster than tube-building in controls, whereas feeding was significantly less in the test than in the control specimens. Test specimens also showed a more vigorous but unquantifiable particle-gathering behaviour. The differences between tests and controls disappeared after completion of tube-rebuilding. Specimens provided with sterile sand showed that tube-rebuilding could proceed without feeding. Gravid, nonfeeding worms, also built tubes.

The two behaviours of tube-building and feeding can therefore proceed independently.

Acknowledgments

We are most grateful to Dr C. Berkeley for his guidance in the initiation of this study. We also thank Dr D. Narver and Mr J. Walker for providing facilities for preliminary work at the Biological Station, Nanaimo. This research was funded by grants from the National Research Council of Canada.

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Dodecaceria berkeleyi n.sp., a Polychaete (Family Cirrutulidae) from New Zealand

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KNOX, G. A. 1971. *Dodecaceria berkeleyi* n.sp., a polychaete (family Cirrutulidae) from New Zealand. J. Fish. Res. Bd. Canada 28: 1437–1443.

The described species of the genus *Dodecaceria* are reviewed. Fourteen species are recognized and their diagnostic characters are given. A new species, *Dodecaceria berkeleyi*, is described from New Zealand where it is found boring in the shells of large gastropod molluscs. An outline is given of the nature of the skin pigments, which are similar to the arenicolochrome of lugworms. Asexual reproduction in the genus is reviewed, and an account is given of autotomy in *D. berkeleyi*, followed by regeneration to give rise to two individuals, a method of reproduction similar to that which occurs in the colonial tube builder *Dodecaceria fistulicola*. An advanced larval stage found in the burrows of *D. berkeleyi* is described.

KNOX, G. A. 1971. *Dodecaceria berkeleyi* n.sp., a polychaete (family Cirrutulidae) from New Zealand. J. Fish. Res. Bd. Canada 28: 1437–1443.

L'auteur passe en revue les espèces du genre *Dodecaceria*. Il reconnaît quatorze espèces et en énumère les caractères diagnostiques. Il décrit une nouvelle espèce de Nouvelle-Zélande, *Dodecaceria berkeleyi*, qui perce des tunnels dans la coquille des grands mollusques gastéropodes. Il donne un aperçu de la nature des pigments cutanés qui ressemblent à l'arénicolochrome des vers rouges. Après avoir passé en revue la reproduction asexuée du genre, l'auteur décrit l'autotomie chez *D. berkeleyi* qui, suivie d'un regénération, donne naissance à deux individus. Ce mode de reproduction est semblable à celui du tubicole colonial *Dodecaceria fistulicola*. Enfin, il décrit un stade larvaire avancé présent dans les tunnels de *D. berkeleyi*.

Received April 14, 1971

THE genus *Dodecaceria* of the polychaete family Cirratulidae is distinguished from the other genera of the family by the possession of a pair of heavily grooved palps and a limited number of paired branchiae on the anterior segments. It was established by Oersted (1843) for the species *D. concharum*, found in galleries drilled into mollusc shells and calcareous algae. A similar habitat has been recorded for the majority of the described species (see below).

Fourteen species of the genus have so far been recorded, seven from the Northern Hemisphere and seven from the Southern; of the latter, two are from southern Africa and four from the west coast of South America. A list of the described species is given (Table 1).

The following are synonyms of previously described species: *D. afra* Augener 1918 p. 468. This species has been referred by Day (1961 p. 500) to the genus *Cauleriella* after examination of the type species; *D. fewkesi* E. and C. Berkeley 1954 p. 308 (new name for *Sabella pacifica* Fewkes, preoccupied). According to Reish (1952), *Sabella pacifica* Fewkes (1889) (preoccupied by Grube 1859) from Santa Barbara, California, is identical with *D. fistulicola* Ehlers (1901) from Chile. Pettibone (1967) points out that if this is accepted then *D. fewkesi* E. and C. Berkeley should also be referred to *D. fistulicola*. Hartman (1959 p. 408) lists both *D. fewkesi* and *D. fistulicola* as valid names. There do not appear to be any valid taxonomic differences separating the specimens described as *Sabella pacifica*, *D. fewkesi*, and *D. fistulicola*, and, in addition, they all have the unique colonial tube-building habit. Reish (1952 p. 104) has given a complete synonymy for *D. fistulicola* up to that date, and also points out that a number of fossil specimens of the species have been ascribed to the genus *Serpula*.

As the genus had not been recorded from the Australasian region it was of interest to find representatives of a new species burrowing in the

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TABLE 1. List of currently accepted species of the genus *Dodecaceria* Oersted, 1843.

Species	Original record	Subsequent record
D. capensis Day 1961 p. 504	South Africa	
D. caulleryi Dehorne 1933 p. 298	France	
D. concharum Oersted 1843 p. 44	Denmark	English Channel, Mediterranean, Black Sea, Bay of Fundy, North Carolina
D. coralli (Leidy) 1855 p. 144.	Eastern United States	
D. diceria Hartman 1951 p. 92	Southwest Florida	
D. fimbriata (Verrill) 1880 p. 177	Bay of Fundy	
D. fistulicola Ehlers 1901 p. 186	Chile	New Caledonia, Western Australia, Red Sea, Western Canada, California, Chile, Pacific Islands, South Africa
D. joubini Gravier 1901 p. 186	Red Sea	Shark Bay
D. laddi Hartman 1954 p. 638	North Marshall Islands	South Africa
D. laddi oculata Hartmann-Schroeder 1962 p. 141	Peru	
D. multifiligera Hartmann-Schroeder 1962 p. 148	Chile	
D. opulens Gravier 1908 p. 41	Peru	
D. pulchra Day 1955 p. 418	South Africa	

shells of the living gastropod (*Cominella adspersa adspersa*) collected by Mr T. Dix in the shallow sublittoral at Kaiteriteri, South Island, New Zealand. Further specimens were recorded by Miss K. Green from the shells of the gastropods *Haliotis iris* and *Cookia sulcata* from the Kaikoura Peninsula.

Genus *Dodecaceria* Oersted 1843

Type (*monotype*) — *Dodecaceria concharum* Oersted 1843. Small polychaetes commonly found burrowing in calcareous encrusting algae or in mollusc shells. Body often flattened and widened posteriorly. Prostomium bluntly conical, usually without eyes and forming a hood over the mouth. Peristomial segment long, achaetous, with a pair of stout grooved palps at its junction with the first setiger; 2–8 pairs of branchiae on the peristomial and the first few setigers. Capillary setae in both the notopodia and neuropodia of the anterior segments. Stout acicular hooks with spoon-shaped ends on a variable number of setigers after the first few.

Dodecaceria berkeleyi n.sp.

Fig. 1–10

Diagnosis — Three, occasionally 4, pairs of annulated branchiae inserted dorso-laterally on peristomium and first 2 or 3 segments; capillary setae only on first 8 setigerous segments and falcate hooks only on a variable number of succeeding segments; capillary setae present in notopodium only of posterior segments.

Description — In life, colour orange to dark green with prominent blood vessel running length of body; palps green, tentacles red to orange. Preserved in alcohol colour is variable, predominantly greyish with darker areas of black pigment. Length of body up to 15 mm; width about 1 mm or less. Number of segments 60–80, closely crowded at rear end of body (Fig. 2).

Prostomium short conical (Fig. 1), somewhat longer than wide, separated from peristomium, which is about twice the length, by an indistinct transverse groove; has a pair of slits at the posterior margin; no eyes have been seen. First segment lacks setae, has a pair of thick, longitudinally grooved palpi inserted ventrolaterally and a pair of slender, annulated, slightly shorter branchiae inserted immediately above at sides of body. Two succeeding setigerous segments each bear a pair of annulated branchiae with last pair slightly longer.

First 8 setigerous segments have only slender, pointed, saw-edged capillary setae (Fig. 3). Capillary setae absent from a variable number of succeeding setigers but present in posterior half of body. Simple falcate hooks (Fig. 4–6) present from 10th setiger; typical segment (20th) has 4 in the notopodium and 3 in neuropodium; stout with typical spoon-shaped ends and in more posterior segments develop a blunt basal spur (Fig. 5).

Records — Numerous individuals obtained from burrows drilled into the shells of the predatory gastropod *Cominella adspersa adspersa* (Bruguière) from the sandy sublittoral at Kaiteriteri and the gastropods *Haliotis iris* Martyn and *Cookia sulcata* (Martyn).

Habitat — All the specimens taken were obtained from burrows either in the shell material or partly in

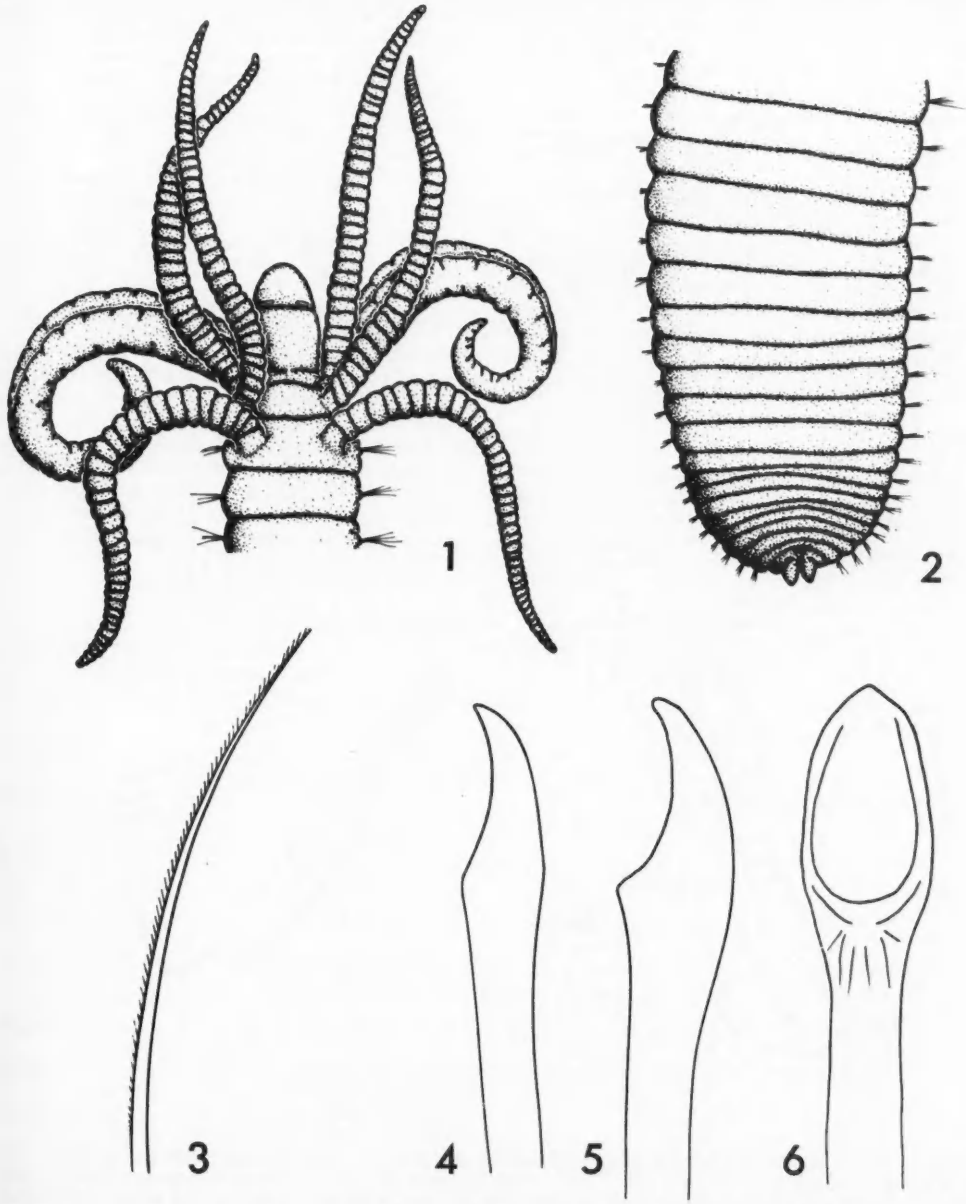
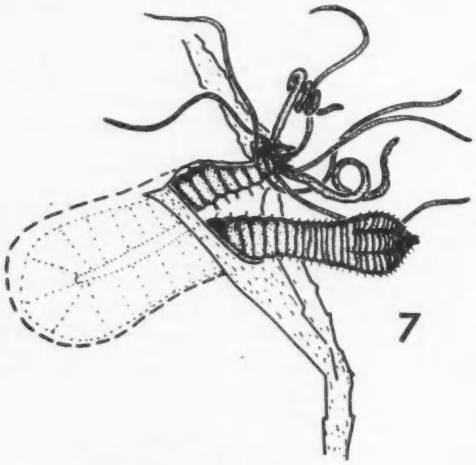
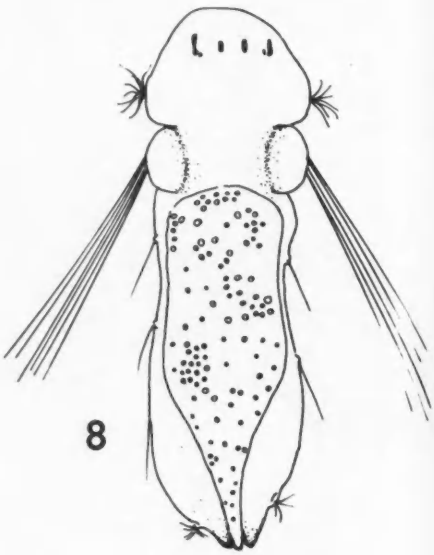
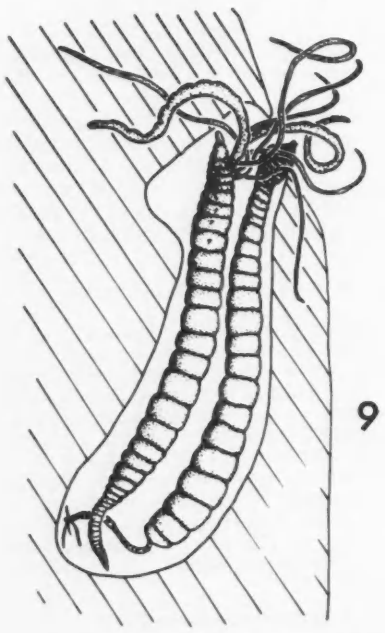


FIG. 1. Anterior end in dorsal view, drawn from life; FIG. 2. Posterior end, drawn from life; FIG. 3. Capillary seta; FIG. 4. Anterior neuropodial hook in lateral view; FIG. 5. Posterior neuropodial hook in lateral view; FIG. 6. Posterior neuropodial hook in lateral view.







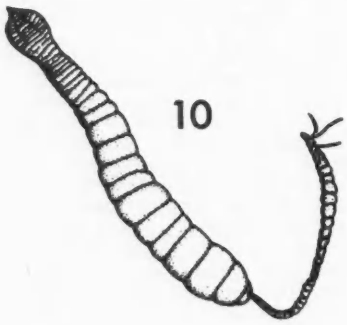


FIG. 7. Worm in tube bent into a U-shape with anterior and posterior ends protruding, drawn from life; FIG. 8. Advanced larval stage taken from a tube; FIG. 9. Worm in tube showing autotomy with regeneration of anterior and posterior ends, drawn from life; FIG. 10. Posterior half of a worm with a regenerating anterior end, drawn from life.

the "lithothamnion" calcareous encrusting algae on the shells of *Haliotis*. The burrows were simple blind ending tubes and in many instances the worms were much longer than the length of the burrows, being bent into a U-shape with both the anterior and posterior ends protruding from the opening (Fig. 7). Berkeley and Berkeley (1954) recorded a similar habit for *D. fistulicola* (= *D. fewkesi*).

Type locality — 0–10 m Kaiteriteri (173°05′N, 48°01′-50″W) South Island, New Zealand.

Holotype and six paratypes — Canterbury Museum, Christchurch.

Remarks

This species is named after Cyril Berkeley and the late Edith Berkeley who added much to our knowledge of the biology of this interesting group. Fourteen species of the genus *Dodecaceria* have so far been described. The diagnostic characters of these species are given in Table 2. Of these, 12 species have been recorded as burrowers in mollusc shells, calcareous algae, corals, and other calcareous structures. One species is colonial, building masses of calcareous tubes, and another inhabits the holdfasts of the large brown alga *Macrocystis*.

Specific differences, as shown in Table 2, are based mainly on the number and arrangement of the pairs of branchiae, the position of the commencement of the acicular hooks, their shape, and their general distribution.

Dodecaceria berkeleyi differs from the other described species of the genus in having three or four pairs of branchiae and in the arrangement of the acicular hooks. *Dodecaceria fistulicola* agrees in that the hooks commence on the ninth setiger but has five to seven pairs of branchiae and differs in other respects. In its mode of asexual reproduction, *D. berkeleyi* resembles *D. fistulicola*, which is, however, a colonial tube-building species.

Pigmentation

Most of the accounts of the species give the colour in life as dark green to dark brown or almost black, with the branchiae and sometimes the palps being light yellow-brown to orange and appearing

Table 2. Diagnostic characters of the species of *Dodecaceria*.

Species	No. pairs branchiae	Commencement of hooks	Habitat	Asexual reproduction
D. capensis	4	Notopodium: 10–13th setiger Neuropodium: 8–11th setiger	Burrows in calcareous algae	
D. caulleryi	4	7th setiger	Burrows in shells and calcareous algae	Schizometamery
D concharum	4–6	7–8th setiger	"	
D. coralli	7	11th setiger	"	
D. diceria	1	11th setiger	Burrows in gastropod shells	
D. fimbriata	3–6	Last 20 setigers	Burrowing in dead shells	
D. fistulicola	5–7	Notopodium: 11–14th setiger Neuropodium: 9–12th setiger	In calcareous tubes built on rock faces in intertidal zone	Autonomy followed by regeneration
D. joubini	6	7th setiger	Burrows in corallines and corals	
D. laddi	2	8th setiger (Hartman) 11–15th setiger (Day 1967)	Burrows in corallines and corals	
D. laddi oculata	1	Notopodium: 5th setiger Neuropodium: 3rd setiger		
D. multifiligera	4	6th setiger	In *Macrocystis* holdfasts	
D. berkeleyi	3–4	9th setiger	Burrows in gastropod shells	
D. opulens	7	8th setiger		
D. pulchra	4–5	Notopodium: 11–12th setiger Neuropodium: 9–10th setiger	Burrows in calcareous algae	

red by transmitted light due to the circulating blood. Berkeley and Berkeley (1954) state that;

"A very strikingly coloured extract is obtained from the worms when they are placed in freshwater or alcohol. Whilst cold the extract has a bright yellow fluorescence. When the aqueous solution is heated, it assumes a deep blue colour. The pigment is extracted by ether from the aqueous solution. It produces dark stains on the skin when the worms are bundled and also stains other organisms associated with them in the colonies."

The same characteristics are shown by the pigments of *D. berkeleyi*. Dales (1963) has examined the skin pigments of *D. concharum* and *D. fistulicola*. He found that the yellow, green fluorescent water-soluble pigments of these species were similar, if not identical, to the arenicolochrome of lugworms.

Asexual Reproduction

Asexual reproduction is now known to occur in three species, *D. caulleryi*, *D. fistulicola*, and *D. berkeleyi*. *Dodecaceria caulleryi* has a unique method of asexual reproduction termed "schizometamery." As described by Dehorne (1933) a portion of the median region of the body separates into individual segments or "schizometameres," each of which gives rise to two buds, which develop and separate as small adults. The "schizometamere" repeates this process and then withers and dies. Thus four new adult animals are formed and the anterior and posterior ends of the original animal regenerate new anterior and posterior ends respectively.

Berkeley and Berkeley (1954) in their account of *D. fewkesi* (=*D. fistulicola*) report a method of asexual reproduction in which individuals undergo autotomy into two halves, each of which regenerates anterior or posterior ends. This mode of reproduction accounted for the observation that colonies that contained sexually mature individuals contained one sex only, each colony presumably being derived by asexual reproduction from a single individual.

A similar method of reproduction occurs in *D. berkeleyi*. Many of the tubes in the shells of *Cominella adspersa* were found to contain both anterior portions with a regenerating tail region and posterior portions with a regenerating head region (Fig. 9). As noted by Berkeley and Berkeley (1954) for *D. fistulicola*, the regenerating portions were very much more slender than the present body portion (Fig. 10) and also bright yellow in colour in contrast to the dark green of the parent body. Regenerating anterior ends also have the palps and branchiae only partially developed. In *D. fistulicola* one of the individuals resulting from this method of reproduction presumably leaves the parent tube and secretes a new one. In the case of *D. berkeleyi*, it is not known how a new tube is excavated in the shell of the host mollusc.

Caullery and Mensil (1898) have recorded examples of regeneration of anterior and posterior regions in *D. concharum*. Asexual reproduction of this type has not as yet been recorded from any of the other species of *Dodecaceria* but it may prove to be a usual method of reproduction in the genus.

Sexual Reproduction

Caullery and Mensil (1898) in their detailed study of *D. concharum* described three forms, one always sedentary and two others in which epitokes also occur. One of the latter (form B) was later made into a new species, *D. caulleryi*, by Dehorne (1933). Caullery and Mensil found that the atokous form (form A) of *D. concharum* reproduced parthenogenetically, the eggs developing within the female to an advanced stage. Parthenogenetic development has not been recorded from any of the other species of the genus, and epitokes are known only from the two species mentioned above. Berkeley and Berkeley (1954) have described the development of *D. fistulicola* (= *D. fewkesi*) through to a 100-hr larva.

A number of the tubes of *D. berkeleyi* in the shells of *Cominella adspersa* from Kaiteriteri were found to contain larvae at an advanced stage of development (Fig. 8).

Acknowledgments

I am indebted to T. G. Dix for the collection of the original specimens from Kaiteriteri and to Miss K. Green for additional specimens from Kaikoura. The assistance of D. Cameron with the illustrations is also gratefully acknowledged.

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Magelona berkeleyi n.sp. from Puget Sound (Annelida: Polychaeta), with a Further Redescription of *Magelona longicornis* Johnson and a Consideration of Recently Described Species of *Magelona*

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JONES, M. L. 1971. *Magelona berkeleyi* n.sp. from Puget Sound (Annelida: Polychaeta), with a further redescription of *Magelona longicornis* Johnson and a consideration of recently described species of *Magelona*. J. Fish. Res. Bd. Canada 28: 1445–1454.

Magelona berkeleyi n.sp. is described from Puget Sound, Washington. It is most similar to *M. filiformis* from Great Britain and *M. lenticulata* from South Vietnam. Detailed studies of *M. longicornis*, utilizing refined dissection techniques, reveal the presence of a number of diagnostic structures heretofore overlooked. Comments concerning the differentiation of nine valid recently described species (since 1963), relative to previously known species, are made.

JONES, M. L. 1971. *Magelona berkeleyi* n.sp. from Puget Sound (Annelida: Polychaeta), with a further redescription of *Magelona longicornis* Johnson and a consideration of recently described species of *Magelona*. J. Fish. Res. Bd. Canada 28: 1445–1454.

Ce texte contient une description de *Magelona berkeleyi* n.sp. recueilli dans Puget Sound, Washington. L'espèce ressemble beaucoup à *M. filiformis* de Grande-Bretagne et *M. lenticulata* du Sud Vietnam. Un examen fouillé de *M. longicornis*, à l'aide de délicates techniques de dissection, met à jour plusieurs caractères diagnostiques jusqu'à présent négligés. On commente la façon dont neuf espèces valides décrites depuis 1963 différent des espèces connues avant cette date.

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AMONG the specimens comprising the collections of Edith and Cyril Berkeley, which were transferred to the National Museum of Natural History (Pettibone 1967), were two lots of magelonid polychaetes. One of them, identified as *Magelona pitelkai*, was unsuitable for study, but the other, identified as *Magelona longicornis*, was most useful in making further more detailed observations of this species than previously was possible (Jones 1963). Additional material, contributing to the new redescription of *M. longicornis*, was made available by Dr K. Banse, University of Washington, and included not only *M. longicornis* but also a new species, *Magelona berkeleyi*, named in honor of Dr Cyril Berkeley.

Since my preliminary revision of the family Magelonidae (Jones 1963), in which I attempted to point out possible diagnostic characters for the various species, some modifications now seem to be in order, based on examination of abundant magelonid material from widespread areas. The tufts of cilia (lateral organs), which were shown in previous figures, are herein omitted. They are present between the neuropodia and notopodia of all magelonids so far observed, and their presence adds nothing to a taxonomic study of the family. Likewise the distributional pattern of granules over the body surface seems not to be of taxonomic significance, since their occurrence and pattern varies so greatly; these also are omitted from illustrations. All magelonids apparently have two paired muscular structures for prostomial support; thus, apart from including them in figures, no further comment concerning them seems necessary.

The terms "lateral" and "medial" lamellae (Jones 1963 p. 2) do not seem to be satisfactory. It is here suggested that the term "lateral lamellae" be maintained for the usually large, flattened structures in both anterior and posterior regions (Fig. 3, 14, 15, 26, 36, and 40, LL). The term "medial lamellae" was originally chosen in deference to the form of these structures in *M. phyllisae* (Jones

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1963 p. 2–5, fig. 6 and 7) where it is, indeed, lamellar. However, in reference to other species of magelonids this is a misnomer. More appropriate terms might be "dorsal medial lobes" in the notopodia (Fig. 3, 15, 26, and 40, DML), "ventral neuropodial lobes" in the neuropodia of the anterior region (Fig. 3 and 26, VNL), and "ventral medial lobes" in the neuropodia of the posterior region (Fig. 15 and 40, VML). Where these processes occur on the ninth setiger, it might be adequate to name them according to their appearance (Fig. 14, VNL, and Fig. 36, VML).

Finally, in the course of studying species closely related to *M. sacculata*, *M. riojai*, *M. obockensis*, and what is presently recognized as *M. papillicornis*, it has been observed that serial structural differences in the parapodia of the anterior region are subtle and important enough to suggest that all of the anterior parapodia (the first to ninth setigers) should be illustrated, as well as representative parapodia of the posterior region.

The descriptions to follow are concerned with one new taxon and one old taxon, both from the North Pacific, *Magelona berkeleyi* n.sp., and *Magelona longicornis* Johnson 1901.

Family MAGELONIDAE Cunningham and Ramage

Magelona berkeleyi n.sp.

Fig. 1–19

Magelona spp. Lie 1968 p. 310. Banse et al. 1968 p. 540.

Differential diagnosis — *Magelona* with tridentate hooded hooks in each fascicle arranged in two groups, vis à vis; prostomium with frontal horns; without specialized setae on the ninth setiger; anterior parapodia with short thick dorsal medial lobes and short ventral neuropodial lobes; ninth setiger without a dorsal medial lobe, neuropodia with lateral lamellae reduced and ventral medial lobes present.

Type locality — Puget Sound, Washington, north of Henderson Inlet (47°10′40″N, 122°48′48″W) (station 6 of Lie 1968), 32–40 m depth, mixed substrate of mud, sand, and gravel.

Material examined — Eight incomplete specimens, all from type-locality, collected on February 13 and May 3, 1963, by K. Banse and U. Lie.

Description — The holotype (USNM 45021) is 14 × 1 mm in the anterior region, for 33 setigers; the figured paratype (USNM 45022) is 16 × 1 mm (26 setigers); and one of the remaining paratypes is 20 × 0.8 mm (36 setigers).

The prostomium (Fig. 1) is broader than long (about 2:1), quite flattened relative to the peristomial region, and bears a pair of rather inconspicuous horns on the anterior margin. In all specimens the prostomium is reflected dorsally so that it is sometimes rather difficult to make out the horns (Fig. 2).

The palps extend at least to the 16th setigerous segment, and, in their distal two-thirds, bear many papillae. More basally, the papillae are disposed in about 8 longitudinally arranged rows and in about 4 rows near the tips.

The first 8 parapodia (Fig. 3–6, 10–13) are similar. The notopodia are raised from the body surface and are provided with rather short thick postsetal dorsal medial lobes and broadly lanceolate postsetal notopodial lamellae. The neuropodia are also raised and bear ventral medial lobes that diminish in size from the first to the eighth setiger. The eighth neuropodia (Fig. 13) are larger and more transversely elongate than those preceding. The setae of the first 8 setigers are all bilimbate, although the second limbation may be inconspicuous (Fig. 7–9). The setal axis does not appear to extend to the limbate tip of the setae. In the first 6 parapodia there are about 18–20 setae in the notopodial setal fascicle and from 15 to 18 in the neuropodial fascicle; these numbers increase through to the ninth setiger where there are about 30 setae in each fascicle.

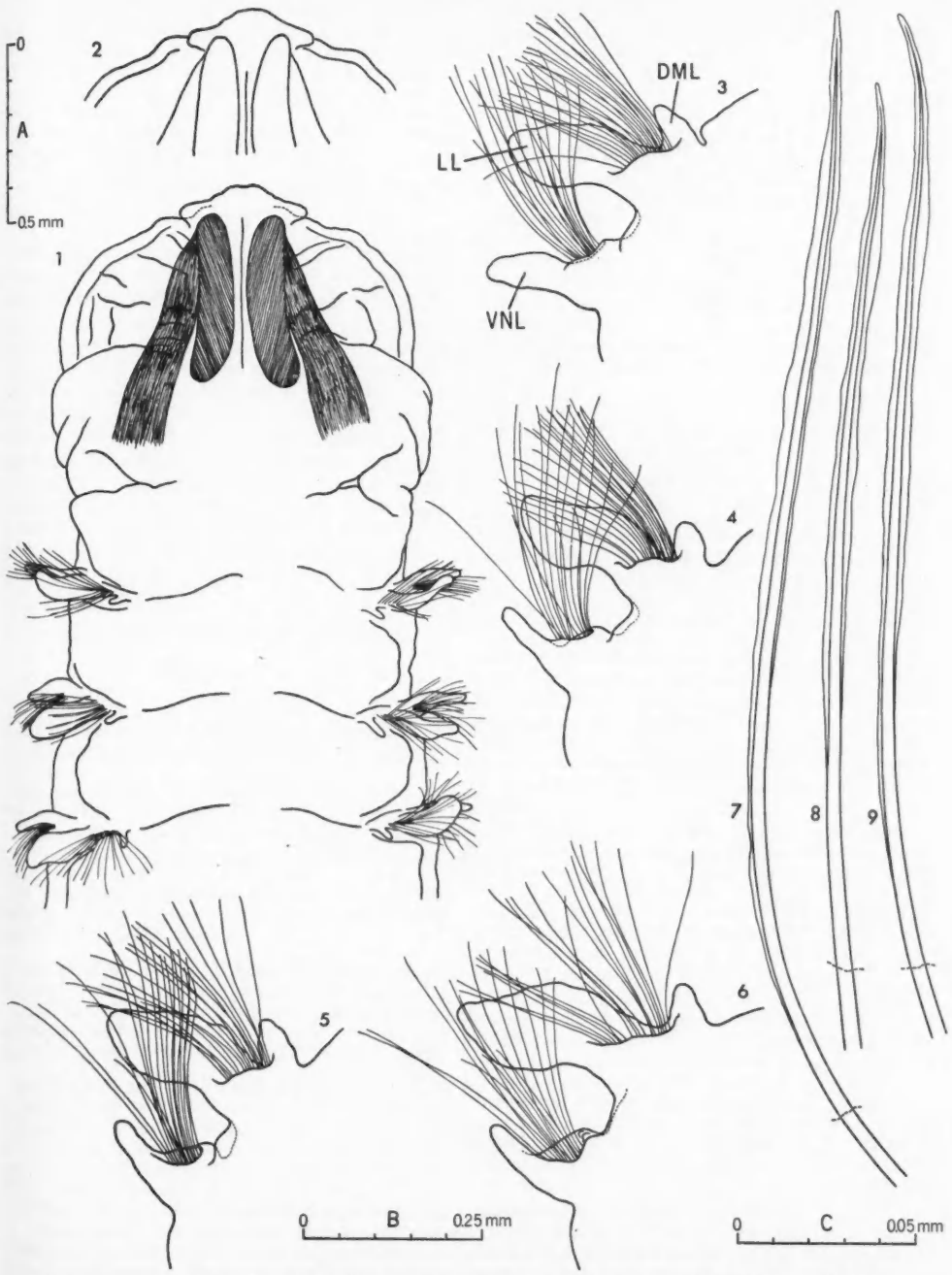
The ninth setiger (Fig. 14) lacks a dorsal medial lobe and the notopodial postsetal lateral lamella tends to be shorter and less lanceolate than those of preceding setigers. The ventral neuropodial lobe is rather well developed, and the upper portion of the neuropodium is developed into a low, broadly based, triangular postsetal lateral lamella. The setae of the ninth setiger are similar to others of the anterior region and there is no marked difference among those that are laterally (Fig. 7), medially (Fig. 8), or centrally (Fig. 9) placed in the setal fascicles.

The parapodia of the posterior region, from the 10th setiger on, are provided with dorsal and ventral medial lobes and lateral lamellae; the former may be low, rounded, and knoblike (Fig. 15) or more cirriform (Fig. 16), and the latter, subcordiform to subovate. The notopodia and neuropodia each have transverse series of about 14 hooded hooks, each of these in 2 series, vis à vis (Fig. 15 and 16). The hooks are tridentate (Fig. 18) with the main fang forming a slightly oblique angle with the main axis (Fig. 17). The most lateral hooks (Fig. 19) are consistently smaller than the others, and those next most lateral may be of intermediate size (Fig. 15 and 16).

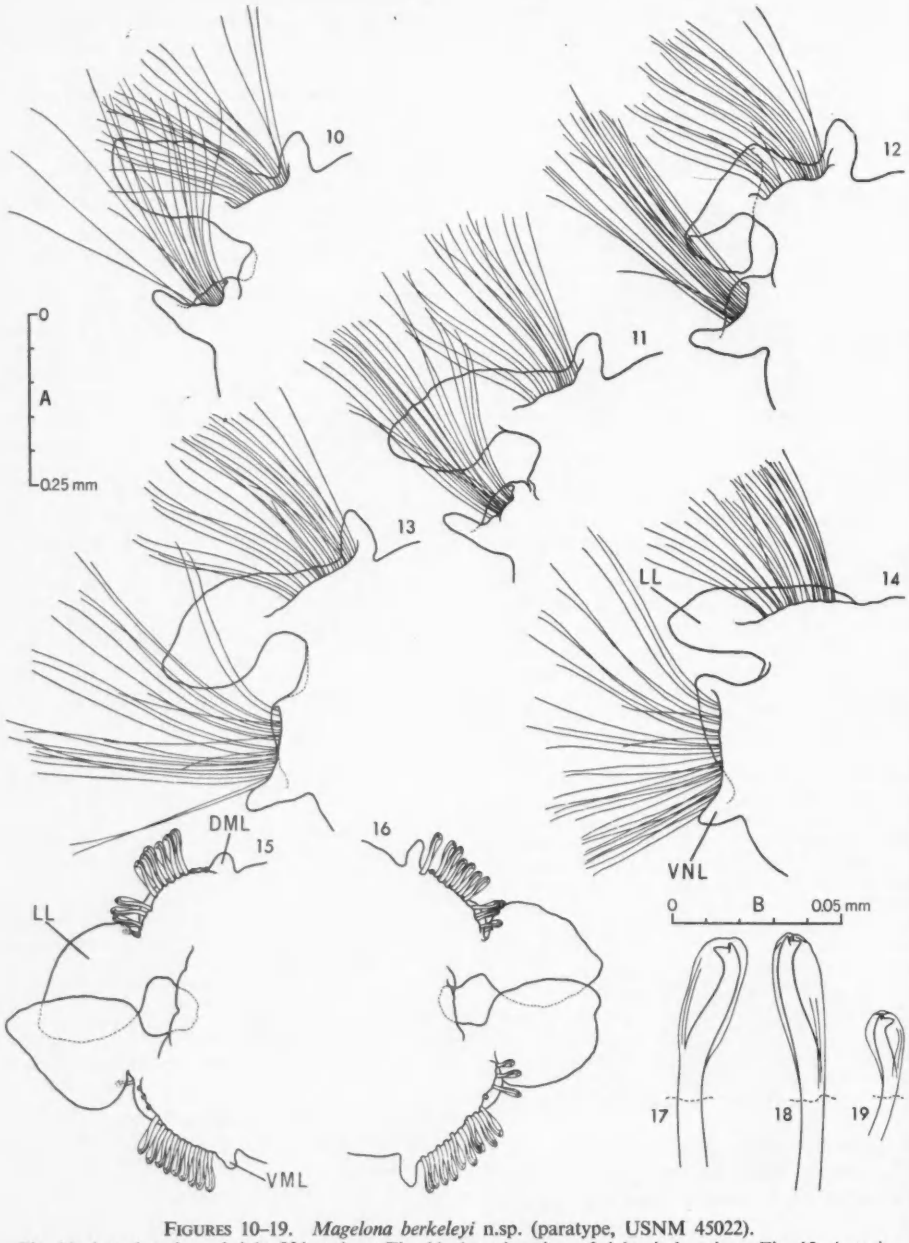
No lateral pouches (Jones 1963 p. 13–14; 1968 p. 275–276) or similar structures were noted in either the anterior or the posterior region.

Etymology — It is with the greatest pleasure that I name this species of *Magelona* in honor of Cyril Berkeley, long time student of the Canadian Pacific polychaetes.

Type disposition — The holotype (USNM No. 45021), the figured paratype (USNM NO. 45022), and three other paratypes (USNM No. 45023, one specimen,



FIGURES 1–9. *Magelona berkeleyi* n.sp. (1–2, holotype, USNM 45021; 3–9, paratype, USNM 45022). Fig. 1. Dorsal view of anterior end, both palps missing (anterior prostomial margin flattened); Fig. 2. Same, not flattened; Fig. 3. Anterior view of right first setiger; Fig. 4. Anterior view of right second setiger; Fig. 5. Anterior view of right third setiger; Fig. 6. Anterior view of right fourth setiger; Fig. 7. Third-most dorsal neuroseta from ninth setiger; Fig. 8. Fifth-most ventral neuroseta from ninth setiger; Fig. 9. Central neuroseta from ninth setiger. 1–2, scale A; 3–6, scale B; 7–9, scale C. LL, lateral lamella; DML, dorsal medial lobe; VNL, ventral neuropodial lobe.



FIGURES 10–19. *Magelona berkeleyi* n.sp. (paratype, USNM 45022).
Fig. 10. Anterior view of right fifth setiger; Fig. 11. Anterior view of right sixth setiger; Fig. 12. Anterior view of right seventh setiger; Fig. 13. Anterior view of right eighth setiger; Fig. 14. Anterior view of right ninth setiger; Fig. 15. Anterior view of right 10th setiger, some hooks broken; Fig. 16. Anterior view of left 26th setiger; Fig. 17. Profile view of neuropodial hooded hook from 26th setiger; Fig. 18. Three-quarter view of notopodial hooded hook from 26th setiger; Fig. 19. Profile view of most lateral neuropodial hooded hook from 26th setiger. 10–16, scale A; 17–19, scale B. LL, lateral lamella; DML, dorsal medial lobe; VML, ventral medial lobe; VNL, ventral neuropodial lobe.

and USNM No. 45024, two specimens) are deposited in the collections of the National Museum of Natural History, Smithsonian Institution. In addition, single paratypic specimens have been deposited in the collections of the British Museum (Natural History), London, Zoological Institute, Academy of Sciences, Leningrad, and the National Science Museum, Tokyo.

Distribution — Puget Sound, Washington, 32–40 m depth.

Discussion — *Magelona berkeleyi* most closely approaches *M. filiformis* Wilson and *M. lenticulata* Gallardo. Diagnostic differences among these three species, in the ninth setiger, consist of subequal short lateral lamellae, in the case of *M. lenticulata* (Gallardo 1968 p. 108 pl. 44 fig. 8); the notopodial and neuropodial lateral lamellae and the ventral neuropodial lobe, all digitate, in *M. filiformis* (Wilson 1959 p. 549 fig. 1H); and a sublanceolate notopodial lateral lamella, a low obtuse triangular neuropodial lateral lamella, and a broadly based triangular ventral neuropodial lobe, in *M. berkeleyi*. In addition, there is a dorsal medial lobe on the ninth setiger of *M. lenticulata*; this structure is lacking in both *M. filiformis* and *M. berkeleyi*.

Magelona longicornis Johnson

Fig. 20–44

Magelona longicornis Johnson 1901 p. 414–415 pl. 11 fig. 115–118. Berkeley, E. 1927 p. 413. Wilson 1959 p. 552–553. Jones 1963 p. 25–27 fig. 61–70. Kitamori 1967 p. 50–51 fig. 2.

Magelona japonica. Berkeley and Berkeley 1950 p. 53. Not *Magelona japonica* Okuda 1937.

Magelona alata Reish 1965 p. 141–143 fig. 2.

Not *Magelona longicornis* Treadwell 1914 p. 206. Ushakov 1955 p. 278–280 fig. 99; 1965 p. 256 fig. 99. [?] Not *Magelona longicornis* Zaks 1933 p. 130. Ushakov and Wu 1962 p. 8; 1963 p. 157 and 163. Levenstein 1966 p. 39, 119, 127.

Differential diagnosis — *Magelona* with bidentate hooded hooks arranged in single series in each fascicle, vis à dos; prostomium with frontal horns; with both dorsal and ventral medial lobes in the posterior region; with dorsal and ventral medial lobes on the ninth setiger.

Material examined — *Washington*: Puget Sound, west of Seattle, Case Inlet, off Johnson Point (stations 2–8 of Lie 1968), January, February, and May 1963, 10–197 m depth, in muds, sands, and gravels, K. Banse and U. Lie collectors, about 180 specimens (USNM 45042–45063); Crescent Beach, near Dutchers Cove, Case Inlet, June 21, 1947, intertidal, sand-gravel beach, M. H. Pettibone collector, one specimen (USNM 45040), one specimen (American Museum of Natural History, uncatalogued, figured in Jones 1963). *British Columbia*: Cardale Point Nanoose Bay, E. Berkeley collector, three specimens (USNM 45041). *Bering and Chukchi Seas*: July and August 1960, 11–67.1 m, in silts and fine sands, J. Tibbs collector, holotype (USNM 30453), three paratypes (USNM 30454), and 11 specimens (USNM 31281–31290) of *Magelona alata* Reish.

Description — Representative specimens consisting of anterior fragments have the following dimensions: 23 × 0.75 mm in the anterior region, for 51 setigers; 20 × 1 mm for 32 setigers; and 17 × 0.75 mm for 36 setigers.

The prostomium is broader than long (approximately 2:1) and is flattened relative to the enlarged peristomial region. The frontal horns are well differentiated from the prostomium proper, their anterior margins varying from essentially smooth (Fig. 21 and 24) to different degrees of crenulation (Fig. 20, 22, 23, and 25).

The palps may extend as far as the 20th setiger and bear up to 8 rows in the proximal papillated area and about 4 rows near the palpal tip.

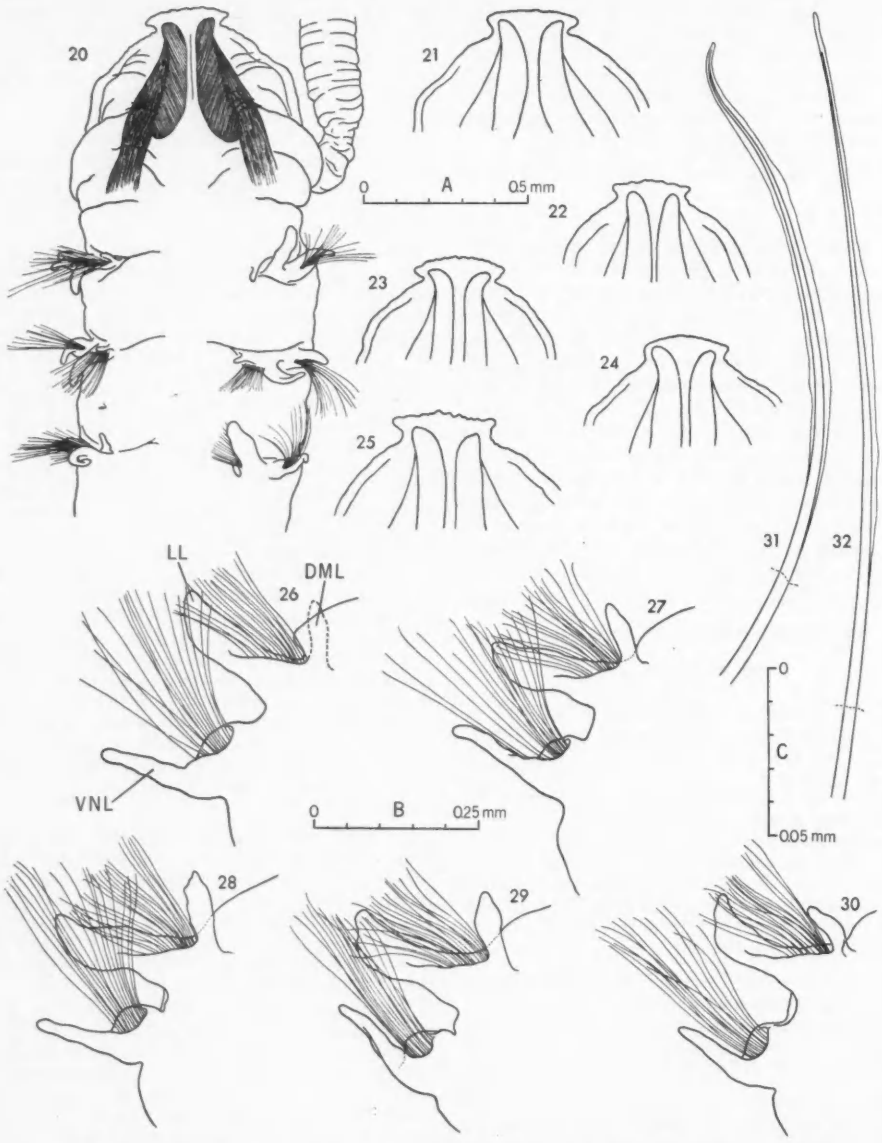
The first 8 parapodia (Fig. 26–30 and 33–35) are basically quite similar. All are provided with a slender presetal dorsal medial lobe and a narrowly lanceolate postsetal lateral lamella in the notopodia and with a ventral neuropodial lobe that becomes shorter from the first to the eighth setiger. In the seventh and eighth neuropodia a postsetal lateral lamella is obscurely developed and the notopodial lateral lamellae are not continuous with the dorsal surface of the body, but with the dorsal medial lobe. The setae of the anterior region are similar and are basically bilimbate, although some appear to be unilimbate (Fig. 31 and 32). In both instances the limbation extends beyond the setal axis. Through the first 7 setigers, there are about 16–20 setae per fascicle; this number increases through the eighth to the ninth setiger where there are about 30 setae per fascicle.

The ninth setiger (Fig. 36) is provided with subequal, rather acutely pointed, elongate, subtriangular postsetal lateral lamellae, a dorsal medial lobe, and a ventral presetal medial lobe. Setae are similar to those of the preceding segments, and, except for a difference in length among those of the neuropodial fascicle, there is no structural difference in their distribution, lateral (Fig. 37), central (Fig. 38), or medial (Fig. 39).

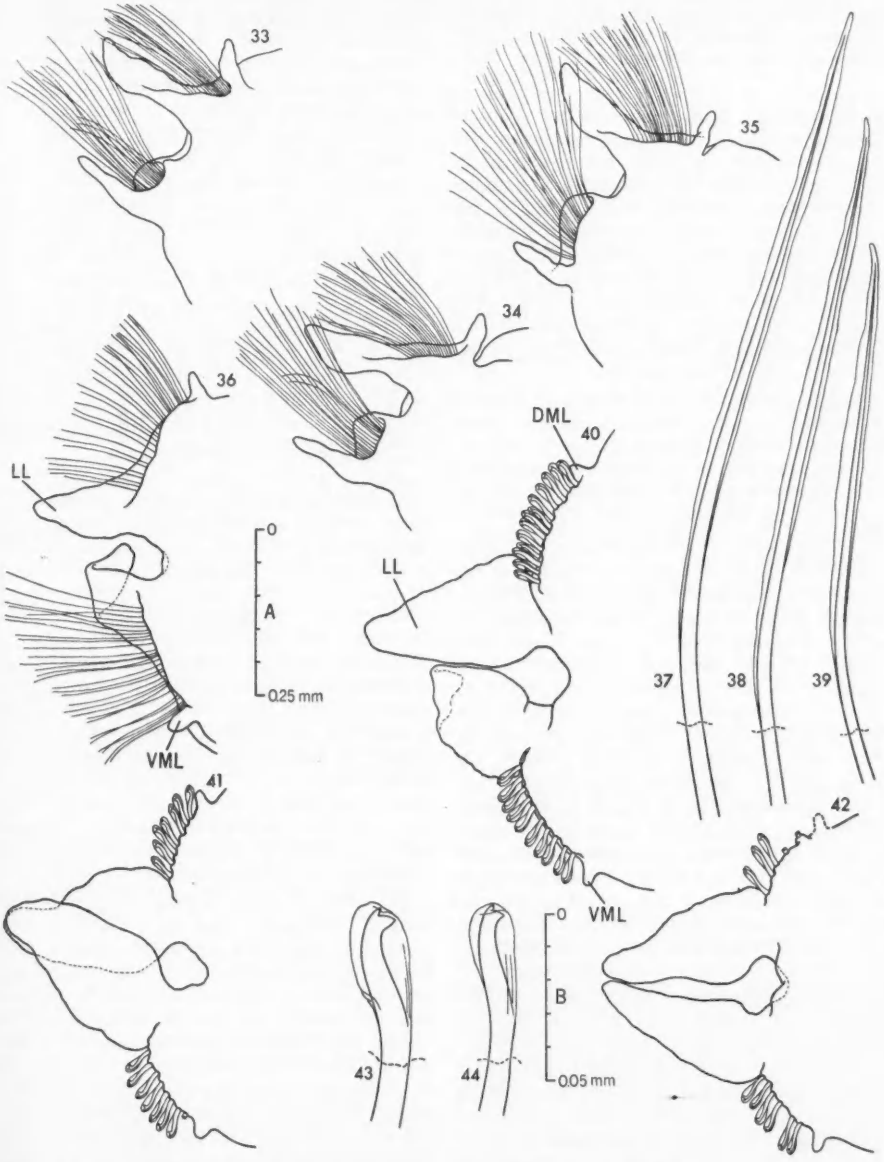
The parapodia from the 10th setiger on (Fig. 40–42) are all provided with elongate, subtriangular lateral lamellae, and small dorsal and ventral medial lobes. All bear rows of bidentate hooded hooks arranged vis à dos in a given series. The number of hooks diminishes from about 12 on the 10th setiger to about 5 more posteriorly. The main fang of the hooks forms a slightly oblique angle with the main axis (Fig. 43, 44). All hooks are about the same size throughout a given series.

No lateral pouches or similar structures were observed throughout the length of the body.

In one instance, a loosely constructed, thin, mucous tube with sand grains adhering to it was found associated with a specimen; it had the same appearance as the tube described for *Magelona* sp. by Jones (1968 p. 292).



FIGURES 20–32. *Magelona longicornis* Johnson (20, USNM 45042; 26–32, USNM 45032).
Fig. 20. Dorsal view of anterior end, left palp missing; Fig. 21–25. Anterior prostomial margins of five specimens; Fig. 26. Anterior view of right first setiger (broken line indicates position and shape of the dorsal medial lobe, lost in preparation; confirmed by observations of its left counterpart); Fig. 27. Anterior view of right second setiger; Fig. 28. Anterior view of right third setiger; Fig. 29. Anterior view of right fourth setiger; Fig. 30. Anterior view of right fifth setiger; Fig. 31. Most lateral notoseta from fourth setiger; Fig. 32. Most medial notoseta from fourth setiger. 20–25, scale A; 26–30, scale B; 31–32 scale C. LL, lateral lamella; DML, dorsal medial lobe; VNL, ventral neuropodial lobe.



FIGURES 33–44. *Magelona longicornis* Johnson (USNM 45043).
Fig. 33. Anterior view of right sixth setiger; Fig. 34. Anterior view of right seventh setiger; Fig. 35. Anterior view of right eighth setiger; Fig. 36. Anterior view of right ninth setiger; Fig. 37. Most lateral neuroseta from ninth setiger; Fig. 38. Central neuroseta from ninth setiger; Fig. 39. Fourth-most medial neuroseta from ninth setiger; Fig. 40. Anterior view of right 10th setiger; Fig. 41. Anterior view of right 17th setiger; Fig. 42. Anterior view of right 31st setiger (broken line indicates position and shape of the dorsal medial lobe, lost in preparation; confirmed by observations of its left counterpart); Fig. 43. Profile view of neuropodial hooded hook from 10th setiger; Fig. 44. Three-quarter view of neuropodial hooded hook from 31st setiger. 33–36, 40–42, scale A; 37–39, 43–44, scale B. LL, lateral lamella; DML, dorsal medial lobe; VML, ventral medial lobe; VNL, ventral neuropodial lobe.

Distribution — Puget Sound, Washington; Vancouver Island, British Columbia; Bering and Chukchi Seas; Japan; from intertidal to 197 m depth.

Discussion — One of the major modifications of the redescription of *M. longicornis* presented herein, compared to my earlier one (Jones 1963), is due to refined dissection techniques. It is somewhat embarrassing to note that I stated (Jones 1963 p. 15), "From personal experience it can be said that it is frequently quite difficult to make parapodial preparations that show the medial lamellae [=dorsal and ventral medial lobes]...," and then (p. 27 fig. 64) described what has proven to be a poorly prepared ninth setiger. I apologize to my colleagues if this has misled them.

It should be noted that the figures accompanying the record of *M. japonica* in the "Canadian Pacific Fauna" (Berkeley and Berkeley 1952 p. 11 and 13 fig. 11–14) are, as the authors state, modified after Okuda and are valid representations of *M. japonica*, but not *M. longicornis*.

Observations on the holotype of *Magelona alata* (USNM 30453) led to the conclusion that this species is a junior synonym of *M. longicornis*.

Although it is not known if the specimens reported by Treadwell from "Kumnes Point, and San Pedro" (1914 p. 206) still exist, observations have been made on a specimen (AMNH 511) identified by Treadwell as *M. longicornis* from "Keins Point, California." This was received by the American Museum of Natural History on March 18, 1912, 1 year before Treadwell's manuscript was transmitted (March 7, 1913). This specimen proves to be *Magelona sacculata* Hartman. In an effort to ascertain the actual source and identity of AMNH 511, a comparison was made of some of the specimens in the collections of the American Museum of Natural History with those listed by Treadwell (1914), through the kind assistance of Ernst Kirsteuer of that institution. No data beyond the species name, locality, and identifier (Treadwell) were available for AMNH 507–520. Of the 13 specimens, apart from *Magelona longicornis*, eight had firm specific determinations and good locality data; there were records for all eight of these in Treadwell's (1914) paper, with the proper locality given. This strongly suggests to me that AMNH 511 is the specimen considered by Treadwell and that a lapsus (Kumnes vs. Keins) was introduced at some point. Even assuming that there was no lapsus, it is not unreasonable to assume that Treadwell was consistent, within a matter of a few years, in his concept of the identity of "*M. longicornis*." It also should be noted that I have been unable to locate either Kumnes Point or Keins Point in either Coast Pilots or navigational charts of that time.

Ushakov's (1955 and 1965) identification of *M. longicornis* from the Sea of Okhotsk was questioned earlier (Jones 1963 p. 27) and examination of his specimens confirm that they are not *M. longicornis* but an undescribed species most closely related to *Magelona obockensis* Gravier.

The listing of the reports of Zaks (1933), Ushakov and Wu (1962 and 1963), and Levenstein (1966) as questionably not *M. longicornis*, stems from incomplete descriptions of the specimens involved.

Magelona longicornis can be differentiated from *M. crenulifrons* Gallardo (1968 p. 100 pl. 44 fig. 1–4) by the possession of dorsal and ventral medial lobes on the ninth setiger of the former (only ventral medial lobes in the latter), as well as its elongate, subtriangular posterior lateral lamellae (as opposed to more ovate lateral lamellae).

Concerning recently described species of Magelona — Since the publication of the key to the then-known species of *Magelona* (Jones 1963 p. 22–23), the following species have been described or designated: *M. equilamellae* Harmelin 1964, Marseille and Villefranche, France; *M. americana* Hartman 1965, off New England, United States; *M. capax* Hartman 1965, off northeastern South America; *M. alata* Reish 1965, Bering and Chukchi seas; *M. wilsoni* Glémarec 1966, southern Brittany, France; *M. agoensis* Kitamori 1967, Ago Bay, Japan; *M. crenulifrons* Gallardo 1968, Nha Trang, South Vietnam; *M. lenticulata* Gallardo 1968, Nha Trang, South Vietnam; *M. koreana* (Okudo) 1937 (as *M. japonica* var. *koreana*), Korean Archipelago (Gallardo 1968); *M. pulchella* Mohammad 1970, Kuwait, Persian Gulf.

Of these, *M. alata* is now synonymized herein with *M. longicornis*, and *M. crenulifrons* and *M. lenticulata* have been considered above. The following comments are based solely on records in the literature. *Magelona equilamellae* (Harmelin 1964 p. 86–88 pl. 9 fig. 1–7) differs from *M. alleni* in that the posterior lateral lamellae of the former are subequal in size, whereas in the latter, those of the notopodia are larger than those of the neuropodia. *Magelona americana* (Hartman 1965 p. 156–158 pl. 30 fig. a–e) and *M. wilsoni* (Glémarec 1966 p. 1079–1081 fig. 1–2) can be differentiated from *M. cincta*, in that the posterior lateral lamellae of *M. cincta* are lanceolate, whereas those of *M. wilsoni* are rounded; *M. americana* has only posterior ventral medial lobes, whereas *M. cincta* has neither posterior dorsal nor ventral medial lobes. *Magelona capax* (Hartman 1965 p. 158 pl. 31 fig. a–d) differs from *M. phyllisae* and *M. longicornis* (with both

posterior dorsal and ventral medial lobes) on the one hand, and from *M. pacifica* and *M. cerae* (with neither posterior dorsal nor ventral medial lobes) in that *M. capax* bears only posterior ventral medial lobes. *Magelona agoensis* (Kitamori 1967 p. 52–53 fig. 5 A–F) contrasts with *M. polydentata* in that the former lacks prostomial horns, whereas the latter possesses them. As reported by Okudo (1937 p. 250–252 fig. 26c) and Gallardo (1968 p. 101), *M. koreana* differs from *M. japonica* in possessing a ventral neuropodial lobe; such a structure is lacking in *M. japonica*. According to Mohammad (1970 p. 305–306 fig. 3–4), *M. pulchella* is most closely related to *M. cornuta*, from which it differs in lacking "branchiae," in details of the hooks, the shape of the papillae, and the form of the ninth setiger. It would suggest that *M. pulchella* is most similar to *M. longicornis* and *M. crenulifrons*, from which it may be differentiated on the basis of the structures associated with the ninth setiger (small "triangular" notopodial lateral lamellae (Mohammad's fig. 3g shows this is an upright ovate lobe), neuropodial lateral lamellae reduced to a "post-setal lip," and the absence of a dorsal medial lobe).

Acknowledgments

I am most grateful to Drs C. Berkeley and K. Banse for making this material available, as gifts to the National Museum of Natural History (USNM); to the American Museum of Natural History (AMNH) for the loan of material; and to M. H. Pettibone for her conscientious and critical reading of the manuscript and her comments.

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Redescription of the Spionid Polychaete *Malacoceros* (*Malacoceros*) *indicus* (Fauvel 1928)

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FOSTER, N. M. 1971. Redescription of the spionid polychaete *Malacoceros* (*Malacoceros*) *indicus* (Fauvel 1928). J. Fish. Res. Bd. Canada 28: 1455–1457.

The co-type of *Malacoceros* (*Malacoceros*) *indicus* has been redescribed. Several discrepancies have been noted with regard to various characters. It is pointed out that use of modern optics in descriptions of setal characters makes it desirable to redescribe certain older species, in order to avoid the establishment of new species that will later have to be synonymized. It is also pointed out that specific characters commonly used for spionids are not necessarily valid for all genera, even though they have been used in the past.

FOSTER, N. M. 1971. Redescription of the spionid polychaete *Malacoceros* (*Malacoceros*) *indicus* (Fauvel 1928). J. Fish. Res. Bd. Canada 28: 1455–1457.

Le cotype de *Malacoceros* (*Malacoceros*) *indicus* est décrit à nouveau. L'auteur souligne plusieurs écarts chez certains caractères. Il recommande la redescription d'espèces anciennes en se servant de l'optique moderne pour la description des soies. Ceci préviendra l'introduction d'espèces nouvelles qui, par la suite, devront être synonymisées. Il remarque de plus que les caractères spécifiques, bien que communément employés dans le passé pour l'identification des spionides, ne sont pas nécessairement valides pour tous les genres.

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FAUVEL (1928) described *Scolelepis indica* as possessing bidentate neuropodial hooded hooks. Later authors (Berkeley and Berkeley 1941; Day 1967) reported the same species but with tridentate hooded hooks in posterior setigers. In a recent study of Caribbean spionids, specimens were found that seem to fit the description of *Scolelepis indica* with the exception that they possess only tridentate and quadridentate hooded hooks.

Fauvel's material was from a collection in the Madras Museum, and earlier attempts by the author to obtain this material were unsuccessful. A specimen designated as co-type, however, is deposited in the British Museum of Natural History. This specimen was examined and found to possess hooks similar to those of Caribbean specimens. Since new species of spionids are often established on the basis of setal characters (determined under high magnification), it is felt that a redescription of the type specimen would in this instance prevent future descriptions of species that might eventually prove to be synonymous. There are also a few statements in the original description concerning other characters that are somewhat misleading.

The following description is based on the co-type in the British Museum and includes some discussion of the specimens from the Caribbean Sea.

Malacoceros (*Malacoceros*) *indicus* (Fauvel 1928)

Fig. 1–6

Diagnosis — Prostomium T-shaped with blunt frontal horns. Irregularly distributed eyespots. Branchiae present from setiger 1 to near end of body. Nipplelike projection on neuropodial lamellae; first appearing on anterior setigers. Tridentate and quadridentate neuropodial hooded hooks first appearing on setiger 37. Pygidium missing.

Description — Body length approximately 80 mm. Prostomium T-shaped, bearing thick, short, frontal horns. Eyespots distributed irregularly on posterior half of prostomium. Posterior of prostomium bluntly rounded and extending to posterior edge of setiger 1.

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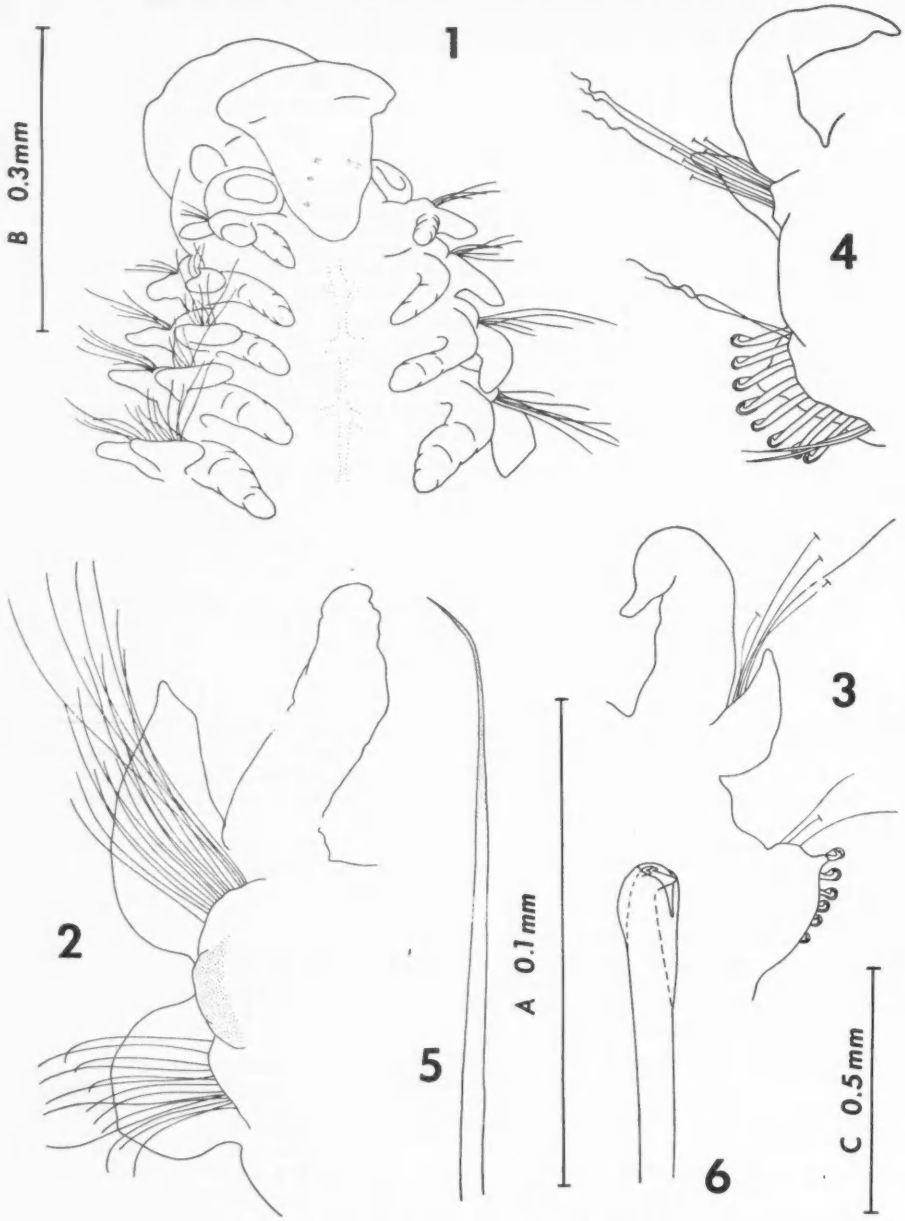

FIGURES 1–6. *Malacoceros* (*Malacoceros*) *indicus*.

Fig. 1. Anterior end, dorsal view, palpi removed; Fig. 2. Right parapodium, setiger 15, anterior view; Fig. 3. Right parapodium, setiger 108, posterior view; Fig. 4. Right parapodium, setiger 163, anterior view; Fig. 5. Anterior neuropodial capillary seta; Fig. 6. Posterior neuropodial quadridentate hooded hook. Scale A, Fig. 5 and 6; Scale B, Fig. 1; Scale C, Fig. 2, 3, and 4.

Proboscis partially everted, bulbous with a pair of lateral glandular structures, 1 on each side, just behind the level of the frontal horns (Fig. 1).

Branchiae appear on setiger 1 and continue to the end of the specimen (pygidium missing). In far anterior setigers they are short and blunt, possibly due to contraction and age of specimen, as this has been noted in older individuals of several species. Branchiae become longer in later setigers and overlap across the dorsum for about 10–15 setigers; behind anterior third of the body they shorten and do not overlap again.

Setiger 1 very well developed, though somewhat smaller and more dorsally situated than those following (Fig. 1). Anterior notopodial lamellae triangular, rounded ventrally and angular at the dorsal tip. Presetal lamellae in anterior setigers continue ventrally between dorsal and ventral rami as a glandular structure (Fig. 2). The notopodial lamellae decrease in size posteriorly until they are about one-third the length of the branchiae (Fig. 3). They eventually become very small, almost digitiform, and are easily overlooked in posterior setigers (Fig. 4). Anterior neuropodial lamellae very rounded and only slightly smaller than those of the notopodia. Eventually a small nipplelike projection appears on the margin (Fig. 2). The presetal lamellae are low and inconspicuous. Lamellae of the posterior setigers are reduced in size with the nipple clearly accentuated at the apex (Fig. 3 and 4).

Anterior setae are all capillaries. Neurosetae arranged in 2 rows with those of the anterior series shorter. Capillaries do not appear to possess a sheath and granulations are confined to the distal portion (Fig. 5). Notopodial setae are similar in appearance and the capillary setae remain generally the same the entire length of the body. Two neuropodial hooded hooks appear on setiger 37. The number increases to 3 on setiger 43 and by setiger 163 there are 7–8 per fascicle. Hooks are tri- or quadridentate; extra teeth, in most instances, are only seen with oil-immersion optics. Hooks possess a single primary hood with an obvious anterior cleft (Fig. 6). There is a small dorsal group of companion setae and 1–2 ventral sabre-setae (Fig. 4).

Pigmented granules are apparent on the body surface and are more concentrated on lamellae and distal tips of branchiae.

Discussion

The original description refers to the appearance of branchiae on the second setiger. This, however, is not the case on the specimen examined, nor is it particularly apparent from the original figure. Branchiae begin on setiger 1.

The co-type and specimens from the Caribbean have neuropodial hooded hooks first appearing on setigers 30–49 (37 on co-type). Fauvel (1928) describes his specimens as having hooks beginning on setiger 70. It is not unreasonable to assume that the range of appearance of hooded hooks could be 30–70, because on Caribbean specimens of *Malacoceros* (*Malacoceros*) *vanderhorsti* (Augener) it is 70–90. It appears from examination of numerous specimens of this genus that it is one of several spionid genera in which the first appearance of hooded hooks is not a good specific character (Foster 1971), because of the wide range found in an individual species. A second possibility, however, is that the hooks on earlier setigers were overlooked by Fauvel as they number only 2–3 per fascicle for about 15 setigers and are not easily seen without high magnification, unless each parapodium is dissected away and observed with a compound microscope.

In this genus one should not place too much emphasis on specific number of teeth on the hooded hooks. On Caribbean specimens and the one described here, one parapodium may contain either tri- or quadridentate hooks or both. Again this is apparently true for certain spionid genera, and it would seem that setal nature is not a good specific character in all genera.

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Seasonal Settlement of Polychaetous Annelids on Test Panels in Los Angeles–Long Beach Harbors 1950–1951

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REISH, D. J. 1971. Seasonal settlement of polychaetous annelids on test panels in Los Angeles–Long Beach harbors 1950–1951. J. Fish. Res. Bd. Canada 28: 1459–1467.

Twenty-four species of polychaetes settled on test blocks suspended at 13 stations in Los Angeles–Long Beach harbors in 1950–51. *Polydora limicola*, *Capitella capitata*, and *Hydroides pacificus* were the three most frequently occurring species. Although a peak in settling occurred during the spring months, in general, the warmer the water, the greater the number of species present. However, *H. pacificus* possessed a summer-full peak, and *C. capitata* exhibited no apparent peak. Many of the species reproduced throughout the year, as indicated by settlement data. A suppression in the number of species was observed whenever the dissolved oxygen concentration was below 4.0 mg/liter.

REISH, D. J. 1971. Seasonal settlement of polychaetous annelids on test panels in Los Angeles–Long Beach harbors 1950–1951. J. Fish. Res. Bd. Canada 28: 1459–1467.

Vingt-quatre espèces de polychètes se sont fixées sur des blocs suspendus à 13 stations dans les ports de Los Angeles–Long Beach en 1950–51. Les trois espèces les plus communes étaient *Polydora limicola*, *Capitella capitata* et *Hydroides pacificus*. Bien qu'un maximum de fixation se produisit au printemps, les espèces étaient généralement plus nombreuses quand la température de l'eau était plus élevée. Cependant, *H. pacificus* accusa un sommet tout l'été, alors que *C. capitata* ne présenta aucun maximum de fixation. Comme l'indiquent nos données, plusieurs espèces se reproduisent à l'année longue. Il y a diminution du nombre d'espèces chaque fois que la teneur en oxygène baisse à moins de 4.0 mg/liter.

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DURING the early part of 1950 several people representing an educational institution, a harbor department, and private industry formed a group that became known as the Southern California Marine Borer Council. Its primary purpose was to learn further of the interrelations of biological, chemical, and physical factors governing the occurrence and distribution of the marine wood-borers. This group initiated a 1-year study in 1950 on the settlement of organisms on submerged wooden test blocks in Los Angeles–Long Beach harbors. The fouling organisms that settled on these test blocks were considered an integral part of this investigation. Previous reports of the results of this study include the accounts of the wood-boring amphipod *Chelura terebrans* and amphipods as fouling organisms (Barnard 1955, 1958) and the seasonal settlement of wood-borers (Menzies et al. 1963).

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The seasonal settlement of marine fouling organisms in general and polychaetes in particular has been summarized by Reish (1961a). The settlement of *Hydroides norvegica* (= *H. pacificus*) was found to be related to the warmer waters in the presence of adequate dissolved oxygen in Los Angeles–Long Beach harbors. Crippen and Reish (1969) found an inverse relation between the number of species of polychaetes on floating wood docks and the water quality. A similar relation was found to exist for animals settling in sediment bottle collections in these harbors (Reish 1961b). Recently suspended test panels have been found useful in relating the settlement of organisms to degrees of pollution (Cory and Nauman 1970; Ignatiades and Becacos-Kontos 1970; and Relini et al. 1970).

The purpose of this account is to report on the seasonal occurrence of the polychaetes that settled on these suspended test blocks in 1950–51. For several reasons it had not been possible to complete this study until now. The recent pollution abatement program in the harbors, especially in Dominguez Channel (Fig. 1), which has resulted in an increase in the amount of dissolved oxygen present in the inner harbor, has been the major

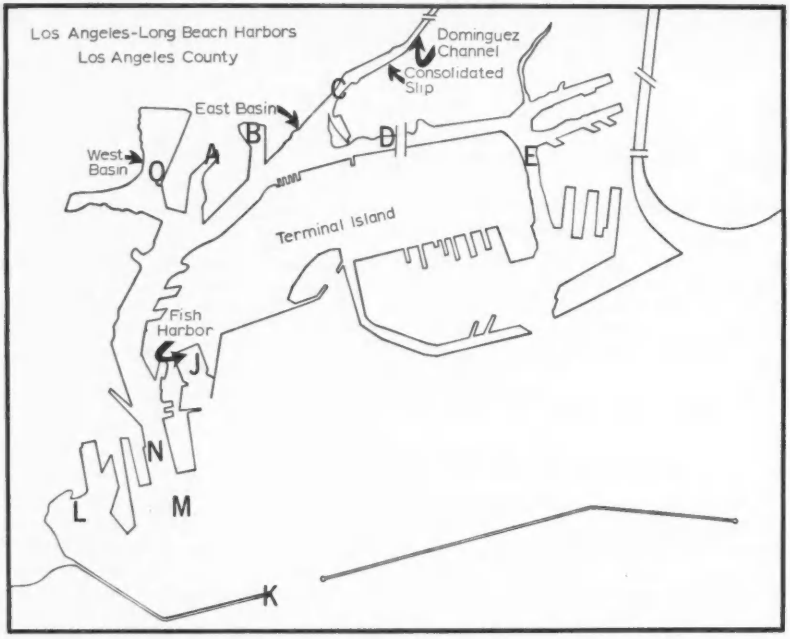

FIG. 1. Los Angeles–Long Beach harbors, California, showing station locations

stimulus to complete this survey. Furthermore, it is hoped that by describing the conditions prior to the clean-up, it will be possible by subsequent surveys to demonstrate the benefit of improvement of water quality through pollution abatement. Polychaetes have been demonstrated to be useful as indicators of varying degrees of water quality here (Reish 1959a; Crippen and Reish 1969) and elsewhere (Henriksson 1969).

Materials and Methods

Test blocks were suspended for 28-day intervals at 13 stations located in Los Angeles–Long Beach harbors for a 393-day period in 1950–51. The first series of blocks was suspended on March 31, 1950, with the initial pick-up on April 28, 1950; each test block was replaced with a new one and the procedure repeated each 28-day period for a total of 13 times with the last series removed on March 31, 1951. Wood blocks were made from Douglas fir and measured 5.1 × 5.1 × 15.2 cm, with a surface area of 362.1 cm^2. A hole was drilled through the block for attachment to a rope. Three blocks were used at different levels at most of the stations; however, only the results from the deep test block are presented herein. This test block was located about 1.0 m above the bottom. Additional details are given in Menzies et al. (1963). The station locations are indicated in Fig. 1, and a brief description of each is given under results below; station numbers used in other studies in the harbors are also given (Reish 1959a).

Biological — After removal, the test was placed in a 1-quart jar and brought back to the laboratory where the fouling organisms were scraped from the block and preserved in formaldehyde. The polychaetes were sorted from this material by the author in 1950–51. Since the amount of fouling organisms varied considerably from station and time to time, a maximum of 15 min was spent with each sample. Therefore, the biological data presented herein are not necessarily the total number of specimens that were present on the blocks, although they do indicate a relative quantitative occurrence of species abundance. The material was stored in alcohol for the ensuing 20 years.

Fifteen stations were studied, as indicated by Menzies et al. (1963), but the polychaetes from stations B (Long Beach Pilot jetty) and P (Los Angeles berth 236) were either not sorted originally or were lost in the ensuing years; therefore, data on the occurrence of polychaetes are available for 13 stations.

Chemical and physical data — Water analyses consisted of dissolved oxygen (Table 1), dissolved oxygen (Table 2), and chlorinity, and they were taken 1.0 m from the bottom each 28-day period. Since the chlorinity was that of normal sea water at all stations but C, these data were not included; the range and mean of the chlorinity data are summarized in Menzies et al. (1963).

TABLE 1. Dissolved oxygen (mg/liter) in Los Angeles–Long Beach harbors 1950–51[a].

Station	4/50	5/50	6/50	7/50	8/50	9/50	10/50	11/50	12/50	13/50	1/51	2/51	3/51
A	1.2	2.9	0.3	0.0	1.0	2.1	0.1	0.1	0.4	1.8	0.5	0.3	3.0
B	3.9	2.4	1.4	1.5	3.5	1.9	0.0	0.2	0.3	1.0	1.2	3.8	3.8
C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
D	5.2	4.1	3.4	3.4	4.3	3.1	0.8	0.8	1.8	1.0	1.6	4.4	4.2
E	6.0	4.7	5.3	5.7	6.7	5.8	4.3	2.5	1.9	2.3	2.4	6.3	4.2
F	6.2	5.8	8.1	6.5	7.5	5.1	4.4	4.2	5.1	4.7	2.7	7.1	7.2
H	4.9	5.8	5.4	4.9	5.9	5.3	0.5	0.1	0.0	2.1	2.7	7.9	5.0
J	4.2	3.4	6.2	3.8	6.0	3.9	0.0	0.0	0.0	0.0	0.6	6.3	4.5
K	6.3	6.6	7.2	6.2	7.3	6.4	3.8	4.6	4.2	6.4	2.5	7.3	2.3
L	7.2	6.5	7.4	4.9	5.8	5.9	2.9	3.4	2.8	4.9	5.0	5.9	3.7
M	7.2	6.4	8.3	5.1	7.4	6.4	3.9	4.4	2.0	5.2	3.2	4.8	5.7
N	5.4	5.3	8.1	4.8	4.9	5.0	1.6	3.5	1.9	4.4	2.5	5.3	5.0
Q	3.9	2.9	2.4	2.6	3.5	3.0	0.1	0.6	0.9	1.3	2.0	3.8	3.4

[a]Readings were taken from approximately 1 m from the bottom.

TABLE 2. Water temperature (C) in Los Angeles–Long Beach harbors 1950–51.[a]

Station	4/50	5/50	6/50	7/50	8/50	9/50	10/50	11/50	12/50	13/50	1/51	2/51	3/51
A	15.6	15.0	17.8	18.7	17.2	18.3	17.8	16.7	16.8	14.7	13.9	13.8	16.9
B	16.1	14.4	18.1	19.8	17.8	19.8	20.6	17.2	16.7	15.3	14.4	13.7	16.0
C	17.5	15.8	20.0	21.6	18.3	20.6	21.1	18.2	18.2	15.6	14.9	14.5	20.6
D	15.5	15.2	18.1	19.7	17.3	19.9	18.7	17.5	16.7	15.3	13.8	13.7	16.8
E	15.7	14.3	19.1	19.0	17.6	19.2	18.7	17.6	16.7	15.6	13.4	12.9	18.0
F	16.0	14.4	19.1	18.7	17.2	19.3	18.7	17.5	16.0	15.2	13.6	13.4	15.3
H	15.3	13.7	16.1	16.7	16.7	18.0	17.8	16.7	14.4	14.4	13.2	12.2	15.0
J	14.1	14.3	18.7	19.2	19.1	18.8	18.7	16.9	16.0	14.6	13.3	12.7	15.6
K	13.1	13.9	17.8	18.3	16.7	18.3	18.3	16.6	15.3	14.5	12.9	12.2	13.8
L	13.9	14.2	19.2	18.3	16.3	18.0	18.7	16.6	16.2	14.4	12.7	12.2	15.2
M	12.7	13.7	18.2	17.5	16.9	18.7	18.7	16.5	16.0	14.2	12.8	12.2	15.1
N	14.4	15.4	18.2	18.1	15.8	18.7	18.3	16.6	16.2	14.6	13.2	12.9	15.4
Q	14.4	17.2	19.4	20.7	20.4	20.6	21.7	18.2	17.8	16.9	14.8	14.9	17.8

[a]Readings taken from approximately 1 m from the bottom.

The mean chlorinity value at station C was 17.8‰. Dissolved oxygen was determined by the Pomeroy–Kirshman modification of the Winkler method (Pomeroy and Kirshman 1945). Temperature measurements were made with a thermistor.

Data

The biological data are summarized in two ways. The principle species are listed by station and their occurrence related to the season, to the total number of species, as well as the chemical and physical conditions of the water. The total number of species taken at each period is included in Table 3. Secondly, the biological data are summarized systematically, in which number of times it occurred at a station and the number of specimens collected are given along with its relation to the season and water conditions.

The dissolved oxygen content and water temperature data are given in Tables 1 and 2, respectively, by station and period.

STATION A

Location — At the innermost part of harbor slip number 1; LA39; *temperature* — 13.8–18.7, 16.9 C; *dissolved oxygen* — 0.0–2.9, 0.5 mg/liter.

A total of 11 species was taken, with a mean of 3 per collection period. *Capitella capitata*, *Hydroides pacificus*, and *Polydora limicola* were the dominant species present. *Capitella capitata* was present during the spring and midsummer 1950 and sporadic thereafter. *Hydroides pacificus* flourished during the warmer water months of July through November 1950. *Polydora limicola* was common from spring through the fall months of 1950. In general, the polychaete population was low during

TABLE 3. Number of species of polychaetes present on test blocks.

Station	4/50	5/50	6/50	7/50	8/50	9/50	10/50	11/50	12/50	13/50	1/51	2/51	3/51	Total no. of species
A	5	8	3	5	3	2	7	1	1	0	1	6	4	11
B	3	4	2	4	1	1	1	1	0	0	0	2	2	5
C	0	1	0	0	1	0	0	0	0	0	0	0	0	1
D	4	3	5	9	5	4	3	2	4	2	4	0	3	14
E	4	3	8	3	3	2	6	6	2	3	4	5	4	14
F	6	4	3	2	3	5	5	1	1	1	3	1	3	11
H	7	1	3	6	1	3	1	1	0	1	2	2	4	13
J	3	2	4	8	4	3	0	0	0	0	0	3	2	10
K	5	0	4	5	4	2	1	2	3	2	4	0	0	10
L	2	2	6	2	0	2	5	2	4	0	2	0	1	12
M	4	3	0	0	4	6	6	0	4	2	4	3	2	10
N	6	0	4	2	3	4	7	3	1	4	8	4	6	13
Q	3	4	6	3	7	4	1	2	3	3	5	5	5	12
Total no. of species	15	11	14	14	10	14	13	10	11	7	12	9	12	

fall into the winter months of 1950–51, the period when the dissolved oxygen concentration was at or below the mean of 0.5 mg/liter the majority of time.

STATION B

Location — Harbor slip number 5, under the wharf at berth 181; near LA45; *temperature* — 13.7–20.6, 16.7 C; *dissolved oxygen* — 0.0–3.9, 1.4 mg/liter.

Only 5 species of polychaetes were taken from the blocks at station B with *Capitella capitata* the only species present more than 50% of the time. Other species include *Polydora liminicola*, *Hydroides pacificus*, *Ophiodromus pacificus*, and 1 specimen of *Autolytus prismaticus*. The majority of the specimens were collected during the spring and early summer months.

STATION C

Location — Near Dominguez Channel entrance to Los Angeles Harbor; LA50; *temperature* — 14.5–21.6, 18.2 C; *dissolved oxygen* — 0.0–0.1, 0.0 mg/liter.

The water quality, as measured by dissolved oxygen, was the poorest, with only one reading of 0.1 mg/liter recorded. A total of 8 specimens of *C. capitella* was collected, 3 in May and 5 in August.

STATION D

Location — Cerritos Channel, eastern side at Ford Avenue bridge; between LA55 and LA23; *temperature* — 13.7–19.9, 16.8 C; *dissolved oxygen* — 0.8–5.2, 3.4 mg/liter.

Stations D and E both had 14 species of polychaetes present, which was the largest number taken from any station. A mean of 4 species was present at station D. *Hydroides pacificus* was the most commonly encountered one from July through January. *Polydora limicola* was present during the spring and again in the late fall winter months.

STATION E

Location — On the fender of the pontoon bridge connecting Terminal Island Long Beach (this bridge has since been replaced with a high one); LB11; *temperature* — 12.9–19.2, 17.6 C; *dissolved oxygen* — 1.9–6.7, 4.7 mg/liter.

A total of 14 species was taken, with a mean of 4 per collection period. *Polydora limicola* was present in every collection but August, with the greater number of species taken in the spring to early summer months. *Armandia bioculata* was common at this station, with a peak in the fall months.

STATION F

Location — United States Naval Operating Base, innermost reaches; *temperature*— 13.4–19.3, 16.0 C; *dissolved oxygen* — 2.7–8.1, 5.8 mg/liter.

A total of 11 species was collected, with a mean of 3 per period. The dominant species, *Polydora limicola* and *Brania limbata*, were abundant from April through September.

STATION H

Location — Seaplane hanger base, United States Navy; *temperature* — 12.2–18.0, 15.3 C; *dissolved oxygen* — 0.0–7.9, 4.9 mg/liter.

Although 13 species were taken from this station, only *Polydora limicola* was present frequently. It was taken every period but December, with peaks before and after the fall lows when the dissolved oxygen levels were at low levels.

STATION J

Location — Fish Harbor at inner breakwater; LA13; *temperature* — 12.7–19.2, 16.0 C; *dissolved oxygen* — 0.0–6.3, 3.8 mg/liter.

Ten different species were collected during the study at station J. *Polydora limicola* was the dominant species at this station, where more specimens were taken than at any other station in the harbors. A population peak occurred in April through September.

STATION K

Location — At entrance to Los Angeles Harbor at United States Lighthouse Service wharf; LA2; *temperature* — 12.2–18.3, 15.3 C; *dissolved oxygen* — 2.3–7.3, 6.4 mg/liter.

Ten species were collected from this station with a mean of 2 per period. *Hydroides pacificus* was the dominating species during the summer and fall months.

STATION L

Location — About 150 m south of the Explorer Base of the Boy Scouts of America; near LA4A; *temperature* — 12.2–19.2, 16.2 C; *dissolved oxygen* — 2.8–7.4, 5.0 mg/liter.

Twelve species were encountered with a mean of 2. *Platynereis bicanaliculata* was the only commonly taken species that occurred in the spring and fall.

STATION M

Location — Channel marker number 5, United States Lighthouse Service; near LA22; *temperature* — 12.2–18.7, 16.0 C; *dissolved oxygen* — 2.0–8.3, 5.2 mg/liter;

Polydora limicola was the dominant species at station M, where 11 species, with a mean of 3, were collected. The occurrence of *P. limicola* was somewhat sporadic with peaks in late summer, early fall, and again during the winter of 1950–51.

STATION N

Location — Los Angeles Harbor berth 70; between LA22 and 26; *temperature* — 12.9–18.7, 15.8 C; *dissolved oxygen* — 1.6–8.1, 4.9 mg/liter.

A total of 13 species with a mean of 4 species was taken from station N. *Polydora limicola* and *Hydroides pacificus* were dominant, with *P. limicola* abundant from July through March, except during the November–December period, and *H. pacificus* abundant during the summer and fall months.

STATION Q

Location — West Basin at berth 147; LA33; *temperature* — 14.4–21.7, 17.8 C; *dissolved oxygen* — 0.1–3.9, 2.5 mg/liter

Twelve species were collected, with *Polydora limicola*, *Hydroides pacificus*, *Capitella capitata*, and *Ophiodromus pugettensis* dominating. Both *P. limicola* and *H. pacificus* were present throughout the period of study, with exception of the October period. *Capitella capitata* and *Ophiodromus pugettensis* occurred during the spring and winter.

Family POLYNOIDAE

Halosydna brevisetosa Kinberg

Halosydna brevisetosa. Berkeley and Berkeley 1948; Pettibone 1953; Hartman 1968; Hillger and Reish 1970.

Occurrence — A(1–2), D(2–2), E(1–2), F(2–2), H2–3), J(3–3), K(5–5), L(2–3), M(2–2), N(2–3), Q(2–2).

Ecology — This species was never commonly encountered on the test blocks. It was present at some stations throughout much of the year with a peak during the months of June through October. Only 5 of the 29 specimens were collected from water having less than 2.5 mg/liter dissolved oxygen. Most of the specimens were taken from the outer harbor stations.

Family CHRYSOPETALIDAE

Paleonotus bellis (Johnson)

Paleonotus bellis. Hartman 1968.

Occurrence — A(5–18), D(4–10), E(4–14), F(1–1), H(2–3), J(4–14), K(3–6), L(1–8), M(3–3), N(2–7), Q(2–4).

Ecology — The seasonal occurrence of *P. bellis* was striking, with over 60% of the specimens taken during June. All but eight specimens were taken from water with a dissolved oxygen concentration of at least 2.5 mg/liter.

Family PHYLLODOCIDAE

Anaitides sp.

Occurrence — E(3–3), H(1–1), L(1–1).

Remarks — Specimens were too immature to permit specific identification.

Eteone sp.

Occurrence — D(1–1).

Remarks — The speciman was too small to permit specific identification.

Eumida sanguinea (Oersted)

Eumida sanguinea. Reish 1959a; Hartman 1968.

Occurrence — D(3–5), E(3–3), H(1–1), L(1–1), M(1–1), N(1–1).

Family HESIONIDAE

Ophiodromus pugettensis (Johnson)

Ophiodromus pugettensis. Hartman 1968.
Podarke pugettensis Johnson. Berkeley and Berkeley 1948; Reish 1959b.

Occurrence — A(5–8), B(3–4), D(1–2), E(1–1), H(1–4), J(3–6), K(1–1), M(1–1), N(4–8), Q(7–19).

Ecology — This species was encountered all months but November and December; a seasonal peak was noted in May and in the following February. Although specimens of *O. pugettensis* were taken in water nearly devoid of dissolved oxygen, most were taken when the concentration was above 1.5 mg/liter.

Family SYLLIDAE

Autolytus prismaticus (Fabricius)

Autolytus prismaticus. Berkeley and Berkeley 1948; Pettibone 1953.

Occurrence — A(2–2), B(1–1), D(2–3), E(2–2), F(2–2), H(1–1), L(1–1), M(3–3), N(3–3), Q(1–2).

Ecology — *Autolytus prismaticus* was very commonly encountered; it was collected generally from at least one station throughout the year from water having at least 2.5 mg/liter dissolved oxygen.

Autolytus sp.

Occurrence — F(1–2).

Remarks — Specimens were too immature to permit specific identification.

Brania limbata (Claparède)

Brania limbata. Fauvel 1923; Reish 1959a.

Occurrence — F(7–17), H(3–5), L(1–1), M(2–2), (N5–10).

Ecology — One-half of the specimens were collected from station F throughout much of the year, with a peak in April and May. *Brania limbata* was never taken from water that had less than 2.5 mg/liter dissolved oxygen.

Exogone lourei Berkeley and Berkeley

Exogone lourei. Berkeley and Berkeley 1948; Hartman 1968.

Occurrence — N(2–2).

Eusyllis transecta Hartman

Eusyllis transecta. Hartman 1968.

Occurrence — D(2–2), E(1–1), N(1–1).

Langerhansia heterochaeta (Moore)

Langerhansia heterochaeta. Hartman 1968.
Syllis (*Ehlersia*) *heterochaeta*. Berkeley and Berkeley 1948.

Occurrence — A(1–1).

Odontosyllis phosphorea Moore

Odontosyllis phosphorea. Berkeley and Berkeley. 1948; Hartman 1968.

Occurrence — D(5–6), H(1–1), J(1–2), K(1–1).

Syllis gracillis Gruke

Syllis gracilis. Fauvel 1923; Berkeley and Berkeley 1941; Reish 1959a; Hartman 1968.

Occurrence — E(1–1).

Typosyllis fasciata (Malmgren)

Typosyllis fasciata. Berkeley and Berkeley 1948; Hartman 1968.

Occurrence — H(1–1).

Family NEREIDAE

Platynereis bicanaliculata (Baird)

Platynereis bicanaliculata. Reish 1959b; Hartman 1968.

Occurrence — D(2–2), E(6–15), F(3–5), H(4–6), J(5–14), K(6–10), L(7–18), M(6–25), N(5–14), Q(3–4).

Ecology — The seasonal settlement of *P. bicanaliculata* was striking; it had a spring peak followed by a low during the warmer months, with indications of another peak starting in March 1951. It was never taken from waters having less than 2.0 mg/liter dissolved oxygen nor from stations A, B, and C. The center of distribution, as based on settlement, was apparently in outer Los Angeles Harbor near station M.

Family DORVILLEIDAE

Stauronereis rudolphi (delle Chiaje)

Stauronereis rudolphi. Pettibone 1961; Richards 1967.
Dorvillea articulata (Hartman). Reish 1959b; Hartman 1968.

Occurrence — A(4–6), F(1–1), J(1–1), Q(1–1).

Family SPIONIDAE

Boccardia proboscidae Hartman

Boccardia proboscidea. Hartman 1969; Crippen and Reish 1969.

Occurrence — D(1–4), L(1–1).

Polydora limicola Annenkova

Polydora limicola. Hartman 1969.

Occurrence — A(9–112), B(6–56), D(8–22), E(11–207), F(9–35), H(12–249), J(8–101 + 4 stations with over 100 specimens each), K(5–8), L(7–53), M(8–58), N(9–125), Q(12–67).

Ecology — Polydora limicola was the most frequently encountered species; it was present at all stations but C and was one of the dominants at nine of the 13 stations. The center of distribution was through the midharbor area. Although *P. limicola* was taken from at least five stations, each collection period throughout the study, its peak in station occurrence and total number of specimens collected was during the spring and summer months. The regression line calculated for the relation of number of specimens and water temperature had a slope of 0.43 and for dissolved oxygen 1.29.

Prionospio pygmaceus Hartman

Prionospio pygmaceus. Hartman 1969.

Occurrence — K(1–7), L(1–1).

Family CTENODRILIDAE

Ctenodrilus serratus (Schmidt)

Ctenodrilus serratus. Berkeley and Berkeley 1952; Hartman 1969.

Occurrence — A(1–1), E(2–2), N(4–5), Q(2–4).

Family CAPITELLIDAE

Capitella capitata (Fabricius)

Capitella capitata. Berkeley and Berkeley 1952; Reish 1959b; Hartman 1969.

Occurrence — A(9–20), B(7–22), C(2–8), D(6–26), E(5–10), F(3–5), H(1–2), J(2–8), K(1–1), M(2–3), Q(8–46).

Ecology — Capitella capitata was a dominant species at stations A, B, and F, and was the only polychaete taken from station C. It was present in about equal numbers throughout the year except during the months of September through October.

Family OPHELIIDAE

Armandia bioculata Hartman

Armandia bioculata Hartman 1938, 1969; Reish 1959b.

Occurrence — A(2–4), D(3–3), E(8–41), F(4–10), H(2–13), J(1–1), K(1–1), L(3–4), M(6–29), N(6–35), Q(2–2).

Ecology — Armandia bioculata was present, with one exception, at least at one station throughout the year; however, population peaks occurred during the warmer months of the year. Most of the specimens were taken in water with a dissolved oxygen concentration of at least 2.5 mg/liter.

Family SERPULIDAE

Hydroides pacificus Hartman

Hydroides pacificus. Hartman 1969.
Hydroides norvegica Gunnerus. Hartman 1961; Reish 1961a (not Gunnerus 1768).

Occurrence — A(7–99), B(4–25), D(8–128), E(5–76), F(4–18), H(1–1), J(1–1), K(7–66), L(2–5), M(7–142), N(8–309), Q(11–388).

Ecology — Hydroides pacificus was second to *Polydora limicola* in occurrence; it was dominant at five stations located in both inner and outer harbor areas. The occurrence of *H. pacificus* was related to water temperature; it was frequently collected during July through November with a peak during October. The regression line for the relation between the number of specimens and water temperature had a slope of 1.92.

Discussion

A total of 24 species of polychaetes was encountered on the test blocks during the 1-year study in 1950–51. Of this total, 10 were commonly encountered: *Halosydna brevisetosa*, *Paleonotus bellis*, *Ophiodromus pugettensis*, *Autolytus prismaticus*, *Brania limbata*, *Platynereis bicanaliculata*, *Polydora limicola*, *Capitella capitata*, *Armandia bioculata*, and *Hydroides pacificus*, with *P. limicola*, *C. capitata*, and *H. pacificus* being the three most important species. *Polydora limicola* was a dominant member throughout the outer harbor, except at the entrance, and in the inner harbor, except at stations B and C. *Hydroides pacificus* was a dominant member at five stations throughout the harbor area during the warmer months, *C. capitata* was a dominant species at stations located in protected waters in basins or channels.

Relation of the number of species to station location — The number of polychaete species present at a station varied from one at station C to 14 at stations D and E (Table 3). The presence of only *Capitella capitata* at station C is the result of little or no dissolved oxygen because of industrial pollution (Reish 1959a). Stations D and E, as well as N, which had 13 species present, were located within the main channel system of the harbors

where water movement is continuous and therefore presumably more likely to have larvae present in the water mass. The stations located at the inner reaches of slips or basins (A, F, H, J, Q), with the exception of station B, had a similar total number of species present. Only five species were taken at station B as compared to 11 at station A and since the median dissolved oxygen was 1.4 mg/liter at B as compared to 0.5 at A and since the water temperature was similar, then it seems logical to assume that some other factor or factors, such as toxic wastes, may play a role in the reduction in number of polychaete species at station B.

Seasonal occurrence — The number of species encountered at all stations during one suspension period varied from 7 to 15 species. Variability in number of species frequently was nearly as great between two successive suspension periods as a seasonal one, but, in general, a greater number of species were encountered during the spring months than during the winter months. These generalities are similar to the settlement of invertebrates in sediment bottle collectors suspended in the same harbors (Reish 1961b).

Among the more frequently encountered species, spring peaks were noted in *Paleonotus bellis*, *Brania limbata*, and *Platynereis bicanaliculata*; a spring–summer peak was observed in *Polydora limicola;* a summer peak was noted in *Armandia bioculata*; summer–fall peak occurred in *Halosydna brevisetosa* and *Hydroides pacificus*; no apparent peaks were noted in *Ophiodromus pugettensis* and *Capitella capitata*. As stated earlier (Reish 1961b), many of the polychaetes in the harbor area either are capable of reproducing throughout the year or possess extended periods, as indicated by the settlement of larvae.

Relation to dissolved oxygen concentration — The inverse relation between dissolved oxygen and the number of species present has been noted previously (Reish 1961b; Crippen and Reish 1969). A suppression in the number of polychaete species on boat docks occurred whenever the dissolved oxygen conditions were below 1.0 mg/liter, and no polychaetes were collected when the level was below 0.3 mg/liter (Crippen and Reish 1969). The relation between dissolved oxygen and the number of species was not as clearly defined as previously observed since as many as five species were taken from a wood block when the dissolved oxygen level was zero. However, when the data for all stations are considered as a unit, a suppression in the number of species is noted below 4.0 mg/liter. The slope for the regression line was calculated to be 0.68 when the data for the number of species present at or below 4.0 mg/liter dissolved oxygen were used. The slope was zero above the 4.0 mg/liter level.

The median dissolved oxygen value was determined for each of the dominant species by noting the amount of dissolved oxygen present whenever the particular species was encountered. Two distinct groups of species were found to exist: the median dissolved oxygen was 2.9–3.2 mg/liter for *Ophiodromus pugettensis*, *Capitella capitata*, and *Hydroides pacificus* and over 4.0 mg/liter for *Halosydna brevisetosa*, *Paleonotus bellis*, *Autolytus prismaticus*, *Brania limbata*, *Platynereis bicanaliculata*, *Polydora limicola*, and *Armandia bioculata*.

Relation to water temperature — Although considerable variation occurred between the relation of the number of species to water temperature, it can be stated, in general, as the water temperature increased, the number of polychaete species settling on the test blocks increased. A slope of 0.60 was obtained when the number of species present per collection period is compared to the median water temperature. A similar relation was found in nearby Alamitos Bay in which there was a direct relation between water temperature and the number of associated species present within the *Mytilus edulis* community (Reish 1964). Undoubtably the interrelation between dissolved oxygen concentrations, as well as other possible factors, and water temperature could alter the number of species present on a test block at any one time.

The usefulness of suspended test panels and a pollution tool has been demonstrated recently by Cory and Nauman (1970); Ignatiades and Becacos-Kontos (1970); and Relini et al. (1970). In these studies, test panels were employed as a monitoring tool. The results reported herein, although they represent data collected over 20 years ago, will be of particular value in evaluating the effects of the pollution abatement program in the inner Los Angeles Harbor area (Reish 1971).

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A New Species, and Additions to the Descriptions of Six Other Species of *Syllides* Örsted (Syllidae: Polychaeta)[1]

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BANSE, K. 1971. A new species, and additions to the descriptions of six other species of *Syllides* Örsted (Syllidae: Polychaeta). J. Fish. Res. Bd. Canada 28: 1469–1481.

Additions are made to the description of *Syllides articulosa*, *S. convoluta*, *S. japonica*, and *S. longocirrata*. *Syllides fulva* and *S. verrilli* are recognized as valid species, and *Syllides benedicti* is newly described. Several new records are given. The overlapping of characters of *Syllides* and *Pionosyllis* is pointed out. Possibly, the insertion of the blades of the compound setae may prove to be a reliable character in differentiating the two genera.

BANSE, K. 1971. A new species, and additions to the descriptions of six other species of *Syllides* Örsted (Syllidae: Polychaeta). J. Fish. Res. Bd. Canada 28: 1469–1481.

L'auteur amplifie la description de *Syllides articulosa*, *S. convoluta*, *S. japonica* et *S. longocirrata*. Il valide *Syllides fulva* et *S. verrilli* et décrit pour la première fois *Syllides benedicti*. Il fait plusieurs mentions nouvelles. Il souligne le chevauchement des caractères de *Syllides* et *Pionosyllis*. L'insertion des lamelles des soies composées est peut-être un caractère valable pour la différentiation des deux genres.

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DIFFICULTIES encountered in identification of species of *Syllides* from Washington waters and Cape Cod Bay, Massachusetts, led to the study of some European material, as well as most specimens of this genus collected on the east coast of the United States and presently deposited in major American museums. Six species are partially redescribed and revised, new records are given, and one new species is erected. A brief discussion of the characters defining *Syllides* and a key for the recognized members of the genus are also provided.

It is a pleasure to dedicate this paper to Dr Cyril Berkeley and thus to acknowledge our indebtedness to him and the late Edith Berkeley. Without their efforts, work on polychaetes in the cool-temperate northeast Pacific Ocean would indeed be discouragingly difficult.

Discussion of Generic Characters

Syllides, a genus of Eusyllinae, was characterized by Örsted (1845) as having clavate (club-shaped) antennae and tentacular cirri (two pairs) and very long articulated dorsal cirri. The latter character holds only after the first segments. Diagnoses by later authors (cf. Fauvel 1923; Day 1967) did not emphasize the length of the dorsal cirri, which in fact is variable, but stressed the absence of a dorsal tooth in the entrance of the pharynx. The closely related genus, *Pionosyllis* Malmgren, is characterized by smooth or pseudo-annulated dorsal cirri and an anterior *Syllis*-tooth in the pharynx. *Streptosyllis* Webster and Benedict, as emended by Southern (1914) has smooth, or very indistinctly articulated dorsal cirri, an unarmed pharynx, and thickened aciculae in some anterior segments. *Pionosyllis* and *Streptosyllis* also have two pairs of tentacular cirri.

Although most species of *Syllides* have club-shaped anterior appendages and articulated dorsal cirri, one (*S. liouvillei* Gravier; preserved) has bottle-shaped antennae and tentacular cirri; some possess smooth dorsal cirri (see key); in others (e.g., *S. verrilli*), the appearance of the dorsal cirri in preserved material is variable. Conversely, *Pionosyllis malmgreni* McIntosh sometimes has almost moniliform dorsal cirri (cf. Day 1967). Further, some species of *Syllides* (the type series of *S. setosa* Verrill; see also pl. 56, fig. 11 in Hartman 1944; and the type series of *S. japonica* Imajima) possess a *Syllis*-tooth or toothlike structures similar to it in their pharynges. A tooth is also

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present in *Streptosyllis cryptopalpa* Hartmann-Schröder, a species with knobbed aciculae in some parapodia and therefore certainly a member of *Streptosyllis*.

The diagnoses of *Streptosyllis cryptopalpa*, as well as of *Syllides japonica*, suggest that the presence or absence of a *Syllis*-tooth is at best a specific character among the Eusyllinae but should not be used for separating genera. As shown, the dorsal cirri alone also do not lend themselves to assigning a species to *Pionosyllis* or *Syllides*. Possibly, the sockets of the compound setae may provide a valid diagnostic character: the blades of the setae of the Syllidae originate between two small processes on the shaft. In all *Syllides* species treated in this paper, these processes are far apart (cf. Fig. 1*l*). In contrast, *Pionosyllis gigantea* Moore, *P. uraga* Imajima, *Odontosyllis phosphorea* Moore, as well as *Syllis* spp. (all from Washington waters), have relatively smaller processes whose distance from each other is much less than the width of the dilated endings of the shafts; in other words, these processes are hidden behind the shafts. An examination of the insertion of the blades of more species is necessary to see whether this is of diagnostic value or is just a function of size of setae. In the *Syllides* species studied here the setae are all quite small (thin).

As a revision of Eusyllinae is beyond the scope of this paper, the conventional views on the extent of *Syllides* are accepted here, and the close study of species is emphasized.

The following abbreviations are used in the text: PA, for Academy of Natural Sciences, Philadelphia, Pennsylvania; NMG, for Naturhistorisk Museum Göteborg, Sweden; SEP, for Systematics-Ecology Program, Woods Hole, Massachusetts; and USNM, for United States National Museum, Washington, D.C.

Syllides longocirrata (Örsted)

Fig. 1

Syllis (*Syllides*) *longocirrata* Örsted 1845 p. 408.

Syllides longocirrata — Webster and Benedict 1887 p. 717. Eliason 1962 p. 241.

Not *Syllides longocirrata* — Langerhans 1879 p. 548. Saint-Joseph, 1887 p. 165; 1906 p. 185. Fauvel 1923 p. 284. Cognetti 1957 p. 35; 1961 p. 298. Banse 1959 p. 430 (for all above, see *S. fulva*). Pettibone 1963 p. 124 (see *S. japonica*). Augener 1913 p. 229. Haswell 1920 p. 102. Marinov 1959 p. 85. Day 1967 p. 259 (for last four, see Discussion).

Types — Inquiries by the present author indicate that the types collected in 1844 in the Oslo fjord are neither in the zoological museums in Copenhagen nor Oslo and are presumably lost.

Diagnosis — Large palps. Median dorsal cirri articulated. Pharynx without tooth. Proventricle through 3½–5 segments. Single simple upper setae on all parapodia, thick and bent in 5 anterior ones, thin and drawn out thereafter. Compound setae of anterior parapodia with rounded shaft endings, pointed thereafter. Upper setae with long blades; medium-sized blades on median parapodia with long basal spurs; both types with pointed tips. Short-bladed setae on posterior parapodia bidentate.

Material studied — Eastport, Maine (cf. Webster and Benedict 1887). USNM 411 (12 specimens).

Skagerrak, sta. 65 of NMG (near Sneholm, Kosterfjord, western Sweden), 100–200 m, clay, spots of solid rock, Aug. 13, 1927 (A. Eliason and R. Wahrberg coll., their sta. 68; A. Eliason ident.). NMG Polych. 11394 (two specimens).

Skagerrak, sta. 27 of NMG (Säcken area, near Hällsö, Kosterfjord, western Sweden), 200 m, clay, Aug. 17, 1927 (A. Eliason and R. Wahrberg coll., their sta. 72; A. Eliason ident.). NMG Polych. 11395. These two records have been mentioned without localities by Eliason (1962).

West Sound, Orcas Island, Wash., approximately 48°36′N, 122°53′W, mud, 40 m, July 1967 (H. L. Sanders coll.), three specimens (two in USNM 45266). The largest animal is 2.6 mm long and has 39 setigers. New record.

Additions to the description — The species has been redescribed by Eliason (1962). Based primarily on the material from West Sound, the following may be added. The unpaired antenna inserts between the posterior pairs of eyes (Fig. 1*a*). The pharynx is chitinized and as long as 3–3½ setigers. The proventricle, with about 25 not readily distinguishable rows of muscular columns, extends through 3½–4½ (5 on Örsted's figure) segments. The tentacular segment is clearly visible dorsally. Anterior dorsal cirri are frequently annulated; posteriorly they are mostly smooth. Ventral cirri on the anterior setigers are short and globular and insert on the outer half of the parapodia (Fig. 1*b*, *c*). The length and also the insertion are changed rather abruptly on setigers 5 or 6 (Fig. 1*d*); thereafter they reach usually beyond the setigerous lobes.

Each setigerous lobe is supported by one acicula with a slightly enlarged tip (Fig. 1*e*). On the 20th foot of the largest specimen, an additional thin dorsal acicula is present (Fig. 1*d*). As already observed by Eliason (1962), the parapodia of the first 5 (or 4) setigers have each an uppermost thick, bent bristle (Fig. 1*f*). This is replaced on the next segment by a thick pointed seta and thereafter by a thin elongated pointed capillary seta, weakly serrated on the concave side (Fig. 1*g*). The number of compound setae is a dozen per foot or slightly more in the first parapodia and falls abruptly to about half this number after the fifth parapodium. The first 5 parapodia bear compound setae that end distally in rounded prongs connected by fine membranes. Figures 1*h–j* show the ends of the shafts seen from the side, after rolling a seta oriented as in *h* upward and thus turning it by 90°,

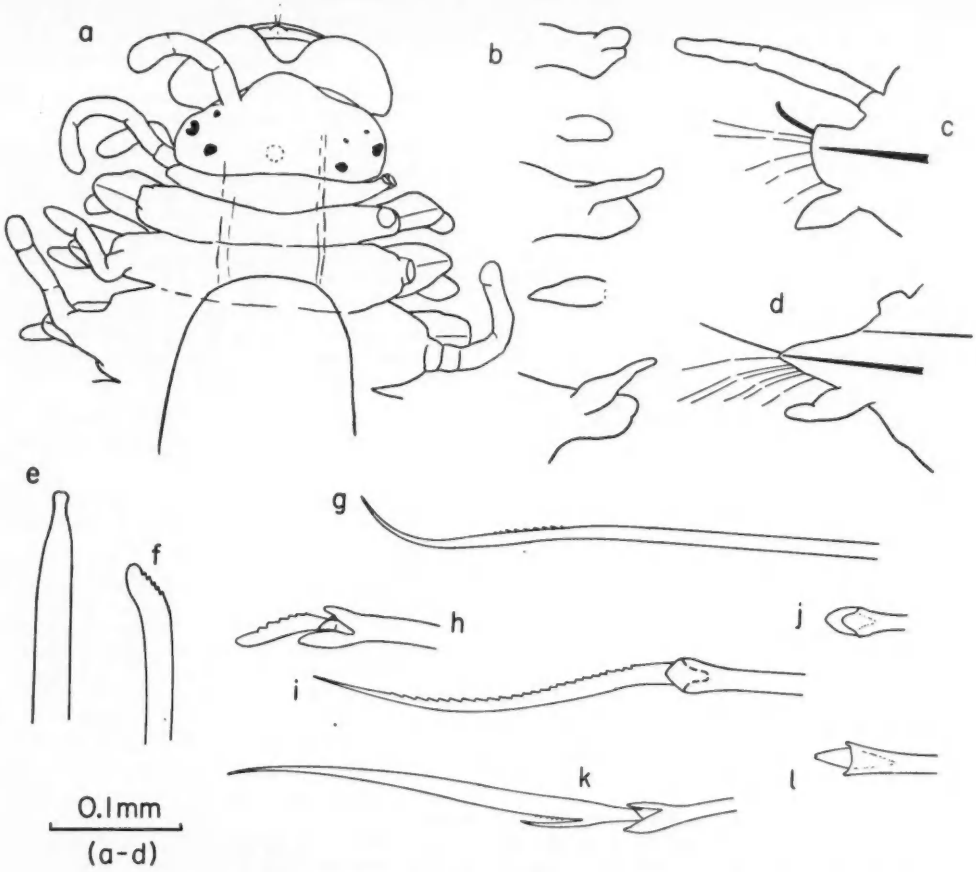

FIG. 1. *Syllides longocirrata* (from West Sound), setae in same scale: (*a*) dorsal view of anterior end, setae omitted; (*b*) ventral views (setae omitted) of first parapodium, fourth ventral cirrus, fifth parapodium, fifth ventral cirrus of other side, and sixth parapodium; (*c*) side view of fourth parapodium, most setae omitted; (*d*) approximately 20th parapodium, dorsal cirrus lost, all setae shown; (*e*) acicula from third parapodium; (*f*) upper simple seta from third parapodium; (*g*) upper simple seta from median foot; (*h, i*) lower and upper compound setae from third parapodium, the shaft of the latter turned by 90°; (*j*) end of shaft of seta as in *h* and *i* seen from the opposite side as in *i*; (*k*) medium compound seta from approximately 20th parapodium; (*l*) end of shaft of seta as in *k* in plane view.

and seen while facing the serration of the blade. The prongs are shorter on the side of the serration of the blades, which is opposite to the usual condition in setae of Syllidae and the posterior setae of this species (Fig. 1*k* and *l*). The blades of the short compound setae (Fig. 1*h*, see also Fig. 1*i*) are blunt and serrated rather than beset with fine hairs or pointed teeth as is usual in syllid setae. A seta with an intermediate-size blade from a median parapodium is shown in Fig. 1*k*; each of these setae has a large single spur at the base of the blade. The tips of the spurred blades seem to be unidentate. Posteriorly, the blades of the upper setae reach a length of 100 μ.

The setae and the insertion of the ventral cirri were carefully studied also in the Swedish material, which was collected close to the type locality, the Oslo fjord, and were found to be identical with those of the Pacific animals. In the material of Webster and Benedict (1887) from Maine the proventricle is somewhat larger than in the European specimens; it extends through 6 or 7 segments and has 45–50 rows of muscular columns. The anterior ventral cirri are formed as shown in Fig. 1*b*; these insert more proximally than those of the European and Pacific animals. The upper simple setae are not as thick as in the other material but are as bent and toothed. The other setae agree.

Discussion — Because of inadequacies of the original description and the loss of the types, there is no proof that the above diagnosis really refers to Örsted's form; it must be noted that *S. benedicti* n.sp. occurs in the same region. Indications for the correctness of the view presented here are provided by the agreement with Örsted's text in regard to the rather short proventricle of the present form, and the observation by Eliason (1962) of pigment on the tentacular segment. Neither character seems especially diagnostic, however (cf. the long proventricle in Webster's material of *S. longocirrata*). The present description includes animals identified by Webster and Benedict (1887) as *S. longocirrata* and agrees with the description by Eliason (1962) of animals from many stations in the Skagerrak. None of the rejected records of *S. longocirrata* refers to *S. benedicti*, the other form Örsted could have had before him.

The rejection of specimens assigned to *S. longocirrata* is based on statements by the authors about the upper simple setae, presence of bidentate blades, and also the length of the proventricle. Especially if an author stated that he looked for upper simple setae but did not observe the strikingly characteristic anterior ones of *S. longocirrata*, it can be assumed safely that they were not present. Therefore, the records from the English Channel listed herein are definitely not *S. longocirrata* (nor *S. benedicti*); moreover, they cannot be assigned to *S. fulva* with any certainty. Likewise, the records by Augener (1913), Haswell (1920), Marinov (1959), and Day (1967) do not refer to *S. longocirrata;* at least some represent undescribed species.

Fauvel (1923) apparently did not use descriptions of *S. longocirrata* as now defined; the records for *S. longocirrata* included in his description refer to *S. fulva*, with the possible exception of that by Saint-Joseph (1887). No author quoted by Fauvel observed a ventral simple seta as contained in his diagnosis. Langerhans (1879), the only author who described a ventral seta in posterior setigers, was not quoted by Fauvel. European records of *S. longocirrata* listed by Cognetti (1957) and Rullier (1963), other than those mentioned among the records of *S. fulva*, cannot be assigned to either species because of insufficient or no information provided. This holds also for the South American record by Ehlers (1897).

Syllides fulva (Marion and Bobretzky)

Fig. 2

Anoplosyllis fulva Marion and Bobretzky 1875 p. 28.

Syllis ochracea Marenzeller 1876 p. 155.

Syllides longocirrata — Saint-Joseph 1906 p. 185. Fauvel 1923 p. 284. Cognetti 1957 p. 35. Banse 1959 p. 430.

?Syllides longocirrata — Langerhans 1879 p. 548. Saint-Joseph 1887 p. 165. Cognetti 1961 p. 298.

Diagnosis — Large palps. Median dorsal cirri articulated. Pharynx without tooth. Proventricle through 5–6 segments. Single simple upper setae similar on all feet, with rounded tips. Compound setae uniform in shape throughout. Shaft endings pointed, blades bidentate, cutting edges proximally with hairs, length varying twofold within parapodia.

Material studied — Near Naples, Italy, a rocky site 1.1 m below low water level, covered by *Halimeda tuna*, without sediment. Aug. 21, 1952 (USNM 45265, one specimen; see Banse 1959; Riedl 1966 p. 37).

Additions to the description — Because of the efforts of earlier authors, especially Marion and Bobretzky (1875) and Marenzeller (1876), only some features need be stressed. The available specimen, which has 40 setigers, is complete except for the pygidium. It is 2.3 mm long and measures at its greatest width 0.32 mm without parapodia and 0.45 mm with parapodia.

The palps are fused at their bases. They are a little longer than the prostomium and close together. They taper toward the tips as shown in pl. 3 fig. 1 of Marenzeller (1876). The very conspicuous brown pharynx, which is not everted in the present specimen, extends through the seventh setiger. The proventricle lies in the next 6 or 7 setigers. The rows of muscular columns, where visible through the body wall, are clearly separated, but their total number (greater than 20) cannot be counted.

The first dorsal cirrus is smooth. The next few are missing, but the one on the seventh setiger is clearly articulated throughout, as is the last preserved one on the 25th setiger. The number of joints in the long cirri is about 15 (one with 19), but it cannot be ascertained whether any cirrus is complete. The first ventral cirrus surpasses the setigerous lobe in side view (Fig. 2*a*). The size of the ventral cirri relative to the setigerous lobes decreases gradually so that at the 20th and 21st setigers (Fig. 2*b*) they are markedly shorter than the setigerous lobes. When, however, the specimen is mounted under a cover glass, these cirri, as well as posterior ones, slightly surpass the setigerous lobes; the anterior ones then appear as conspicuous as in pl. 2 fig. 8 of Marion and Bobretzky (1875).

The aciculae occur singly and are pointed (Fig. 2*c*). A simple dorsal seta, faintly serrated on the convex side (Fig. 2*d*), is present in all setigers. The distal diameter is uniform (3 μ), whereas that of the distal shaft of the compound setae in the first setiger is about 2 μ and in the 20th–21st setigers is 3 μ. All compound setae are of the same form. The ends of the shafts, when seen from the back (in relation to the cutting edge of the blade, Fig. 2*e*) have two prongs. In side view, the ends of the shafts are serrated (Fig. 2*f*) except on the first setiger, where they are inconspicuously serrated. Regardless of the length of the blades, they are bifid at the tips and have

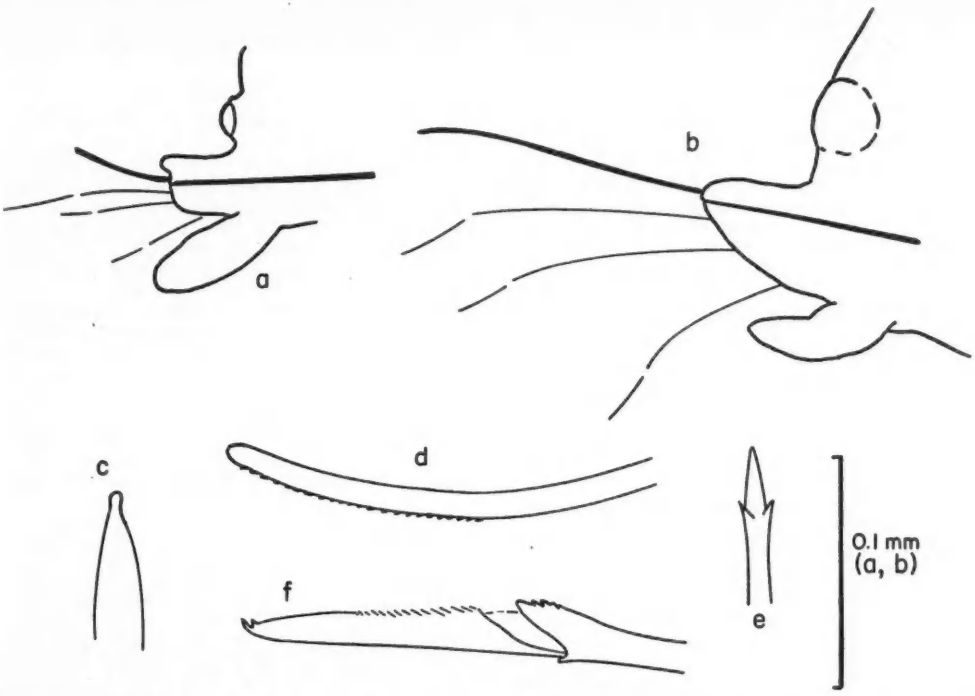

FIG. 2. *Syllides fulva*, setae not to scale: (*a*) first foot, most compound setae omitted; (*b*) 21st foot, most compound setae omitted; (*c*) acicula from first parapodium; (*d*) simple dorsal setae from first parapodium; (*e*) end of shaft of compound seta in plane view; (*f*) compound seta with medium-long blade from 21st foot.

fine hairs of equal length on their basal halves. These hairs could not be seen on the setae of the first setiger, where also the tips of the blades have only very fine secondary teeth. The length of the blades varies from 40 to 20 μ on the first setiger and from 30 to 15 μ on the 20th–21st setigers. About two each of the shortest and longest setae are found on a foot; 10 setae with blades of intermediate length occur on the first setiger and about a dozen, on the median and posterior segments. Ventral simple setae are not present.

Discussion — Webster and Benedict (1887), Cognetti (1957), and especially Eliason (1962) have pointed out differences between the Mediterranean records and typical *S. longocirrata* (Örsted). Comparison of specimens of *S. longocirrata* and *S. fulva* shows that the latter form is certainly distinct.

The synonyms and records are based on statements by the authors on the form of upper simple setae, the observations of bidentate blades in the compound setae, and also the length of the proventricle, which is, however, a less reliable character. Records of *S. longocirrata* from the English Channel were previously rejected herein. These might possibly represent *S. fulva*, but small differences between animals from the English Channel and from the Mediterranean pointed out by Saint-Joseph (1887) and Cognetti (1961), as well as the change in habitat stressed by the latter author, should not be overlooked. Possibly a form different from the typical *S. fulva* occurs in the English Channel. It is not *S. benedicti* n.sp., because, as observed by Saint-Joseph (1887), the upper simple setae start on the eighth rather than the first setiger as in *S. benedicti*. Because of the presence of ventral simple setae, the record from Madeira by Langerhans (1879) also may refer to another species — although certainly not to *S. longocirrata*.

Syllides setosa Verrill

Syllides setosa Verrill 1882 p. 369; pl. 56 fig. 11 in Hartman 1944. Hartman 1942 p. 14.

Not *Syllides setosa* — Pettibone 1963 p. 126 (see *S. verrilli*).

Types — The types collected at the water surface near Woods Hole are apparently lost: they are not deposited in the Museum for Comparative Zoology, Harvard University, Cambridge, Massachusetts; the USNM; nor at Yale University, New Haven, Connecticut (cf. Hartman 1938, 1942). Inquiries by the present author indicate that neither are they deposited at the PA, The American Museum of Natural History, New York, N.Y., nor the Gray Museum associated with the Marine Biological Laboratory, Woods Hole, Massachusetts.

Material studied — None.

Discussion — Without the types, the species cannot be fully characterized. Its salient features are: large size, about 50 segments. Clavate antennae and anterior dorsal cirri. Other dorsal cirri articulated. "Palps short, often not visible from above; below they appear as flat lobes" (cf. Verrill 1882 p. 369). They are larger than the minute ones of *S. verrilli* (Verrill 1882 p. 369). The pharynx can have a tooth according to Verrill. The distal ends of the shafts of the compound setae have conspicuous single subapical spines (cf. pl. 56 fig. 11*b* and *c* in Hartman 1944), similar to those of *S. verrilli* and *S. benedicti*. Swimming setae begin in Verrill's largest specimen singly on the eighth or ninth setiger and occur in bundles from the 18th (drawn as bundles from the eighth setiger, pl. 56 fig. 11 in Hartman 1944).

As stated also under *S. verrilli*, I differ from Pettibone (1963) in not considering that species as a synonym of *S. setosa*. A specimen identified by Verrill as *S. setosa* is referred to *S. japonica*.

Syllides convoluta Webster and Benedict

Fig. 3

Syllides convoluta Webster and Benedict 1884 p. 709. Not *S. convoluta* Webster and Benedict 1887 p. 717 (see *S. benedicti* new species).

Types — Syntypes, from Race Run, near Provincetown, Massachusetts, intertidal sand, USNM 412 (four specimens on four slides).

Diagnosis — Large palps. Median dorsal cirri articulated. Pharynx without tooth. Proventricle through 3½–4 segments. Single simple dorsal setae similar on all parapodia, with split tips. Shaft endings of compound setae pointed throughout, with single large subapical spines. Length of blades varying by a factor of 2 or less within median parapodia.

Material studied — Syntypes.

Additions to the description — All syntypes are relaxed (cf. Webster and Benedict 1884 pl. 2 fig. 12). None seems to be mature. Three conspicuous pairs of eyes are present in all specimens. The antennae are almost smooth. The few preserved dorsal cirri have about a dozen articles. The ventral cirri are elongated from the first foot onwards, reaching slightly beyond the setigerous lobes, and insert in the outer third on all parapodia. The pharynx extends through 2½–3½ segments. The proventricle is as long as 3½–4 segments and has approximately 30 rows of muscular columns.

The aciculae (one per parapodium) have cuplike tips (Fig. 3*a*). Single upper simple setae occur from the first setiger. Their tips are slightly enlarged and split in a fairly regular manner (Fig. 3*b*). The distal endings of the shafts of the compound setae are uniform throughout the body and have single large subapical spines (Fig. 3*c*, *d*). The blades are of the general outline shown in *c*; their length varies between 35 and 15 μ within median feet. Because the mounts were not quite satisfactory, I could study only two animals with an oil-immersion lens. Hairs on the cutting edges of the blades could not be discerned; if present, they would be very fine. Also, subapical teeth could not be seen at the tip of the blades, and if present throughout, must be minute. Because a spur at the base of the blades can be recognized in other species under good optical conditions even with a 40×

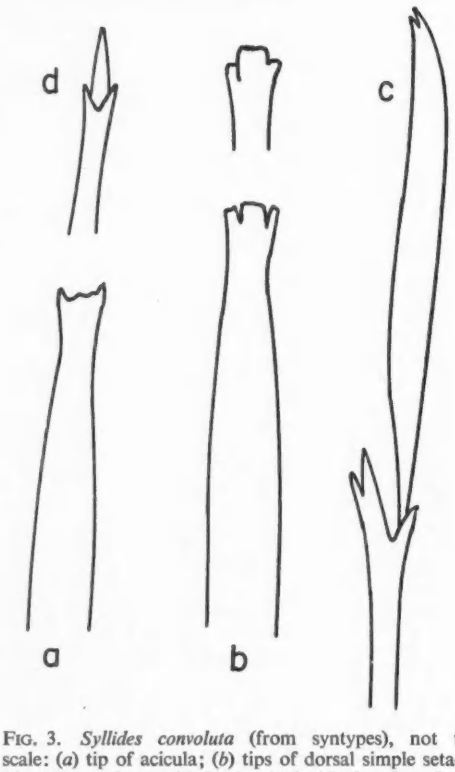

FIG. 3. *Syllides convoluta* (from syntypes), not to scale: (*a*) tip of acicula; (*b*) tips of dorsal simple setae; (*c*) compound seta, blade sketched; (*d*) tip of shaft of compound seta in plane view.

dry objective, but could not be found upon searching with an oil immersion, it also is apparently absent.

Remarks — As implied, I consider *S. convoluta* a valid species in contrast to Pettibone (1963), who included it in *S. longocirrata*.

The syntypes have up to 35 setigers (complete specimens) and 2.5 mm length. The largest animals observed by Webster and Benedict (1884) had 50 segments. The length given (25 mm. Webster and Benedict 1884 p. 710) must be an error, as shown by the stated width of the animals, which is similar to that of the syntypes, the drawings in that paper, and the remark about the types in their publication of 1887 (p. 717, under *S. convoluta*).

Syllides articulosa Ehlers

Syllides articulosus Ehlers 1897 p. 42. Hartman 1964 p. 89 (for earlier records). Hartmann-Schröder 1965 p. 111.

Diagnosis — Palps large. Median dorsal cirri articulated. Pharynx without tooth. Proventricle through 6–10 segments. Single simple upper setae on median and posterior parapodia, pointed. Blades of compound setae with finely serrated cutting edges, bidentate on median parapodia, very long anteriorly; length varying within anterior and median parapodia by a factor of approximately two.

Material studied — Dr G. Hartmann-Schröder kindly inspected the syntypes from southern South America at the Zoological Museum of the University of Hamburg.

Additions to the description — According to a letter by Dr G. Hartmann-Schröder, the uppermost setae in the syntype with swimming setae are anteriorly pointed but bidentate on median and posterior parapodia. All other blades are bidentate. Even the uppermost blades are dorsally broad, and not *Ehlersia*-like as stated by Monro (1939). The blade of the uppermost compound seta on the second parapodium is 232 μ long, that of the lowermost seta measures 123 μ. The blades of these setae on a median parapodium are 123 and 49 μ long, respectively. The blades on posterior parapodia have practically the same length as those on the median parapodia.

Regarding the occurrence of the upper simple seta, the diagnosis and the description by Ehlers (1897) contradict each other. Augener (1932) observed these setae in material from South Georgia only on the median and posterior parapodia. According to another letter by Dr G. Hartmann-Schröder, the occurrence in the type series is quite irregular. In one specimen with swimming setae, they are found from the first and fifth parapodia, in another one from the seventh. In an animal without swimming setae, the simple setae start on the 19th setiger. In any case, they are present also on the posterior segments, but may be irregularly absent on median ones.

Syllides verrilli Moore

Fig. 4

Syllides verrilli Moore 1908 p. 448.

Syllides setosa — Pettibone 1963 p. 126.

Types — Holotype, PA 2402, from surface collection at Woods Hole, Massachusetts, July 3, 1905. Paratype, PA 2401, same locality and date.

Diagnosis — Palps minute. Median dorsal cirri articulated. Pharynx without tooth. Proventricle through 4 (5) segments. Single simple upper setae on all parapodia, with bifurcated tips. Compound setae anteriorly with rounded shaft endings, in side view homogomph; heterogomph and pointed on median and posterior parapodia. Shaft endings usually with single large subapical spines. Blades bidentate, with hairs on cutting edges; length variable. A small species.

Material studied — Type series.

Woods Hole, Mass; the specimen recorded as *S. setosa* by Pettibone (1963). USNM 33155.

Wild Harbor Marsh, Buzzards Bay, Cape Cod, Mass., intertidal, Oct. 2, 1969 (J. F. Grassle coll.; sample SS IV B.S. 17, about 10 specimens).

Wild Harbor, Buzzards Bay, Cape Cod, Mass., 12 m, Nov. 13, 1969 (J. F. Grassle coll.; sample SS 7 B.S. 43, 43 specimens).

Same, nearly 10 m, Aug. 11, 1970 (J. F. Grassle coll.; sample SS 9 B.S. 145, about 25 specimens). All specimens from Buzzards Bay were lent by Dr J. F. Grassle, Woods Hole Oceanographic Institution; these records have not been published before.

Cape Cod Bay, Mass., station SEP 1608–E3, approximately 41°53′N, 70°03′W, 6 m, Sept. 6, 1967 (one specimen). New record.

Additions to the description — The types, received only after the following description was made, were especially checked for their upper simple and their compound setae.

Although the numerous specimens from Buzzards Bay were collected on the bottom, most bear swimming setae. Most have 25–26 setigers, but some mature animals have only 21 setigers and are about 1.5 mm in length (normal contraction of the body). In contrast, an animal with 30 setigers did not have swimming setae. The animal from Woods Hole (cf. Pettibone 1963 fig. 36a p. 125) caught in the plankton has 28 setigers; it is 2.3 mm long and 0.2 mm wide (without parapodia).

The antennae are sometimes articulated; the approximately 10 articles are twice as wide as long. To judge from the other Eusyllinae, this is a pseudo-articulation. Also, the ventral parapodial cirri sometimes appear to consist of three articles. The tentacular segment is usually separated from the prostomium and the following segment. Dorsal cirri are beaded usually from the fifth setiger.

The aciculae have knoblike tips (Fig. 4*a*). The simple setae are conspicuous, approximately 1.5 times as thick as the shafts of the compound setae, and appear bifur-

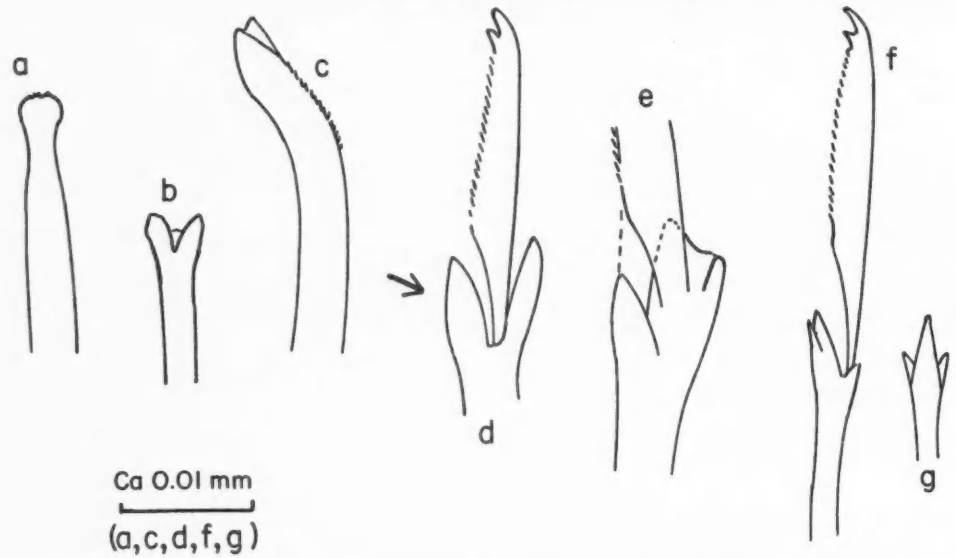

FIG. 4. *Syllides verrilli* (*a*, *f* from specimen from Buzzards Bay, the others from USNM 33155): (*a*) acicula; (*b*) dorsal simple seta under low power, in plane view; (*c*) dorsal simple setae in side view; (*d*, *e*) ends of shafts of compound setae of third setiger, *d* in side view, *e* slightly turned and enlarged; the arrow in *d* indicates the position of the subapical spine present in other specimens; (*f*) compound seta with short blade from median segment; (*g*) shaft endings of compound seta from median segment in plane view.

cated even under low magnification as shown by Moore (1908 fig. 2d) and Fig. 4*b*. In side view, under high power, the setae appear bent and slightly serrated (Fig. 4*c*). On a few anterior segments (6 in holotype, less in other specimens), the shafts of the compound setae have long rounded prongs where usually the inconspicuous socket for the blade is found (Fig. 4*d*, *e*); the form of the end of the shaft is very similar to that in *S. longocirrata* except that the seta of *S. verrilli* usually has a subapical spine (cf. Fig. 4*f*). The spine can be absent (as anteriorly in USNM 33155, Fig. 4*d*) or barely discernible, probably because of wear and tear. Under low power the anterior setae appear homogomph.

The blades of the compound setae are bidentate and have coarse hairs on the cutting edges. The blades of 4 or 5 upper setae on the third setiger of one specimen are 50–60 μ long, whereas the blades of the about 15 lower setae are shorter (about 20 μ in the lowermost ones). On a median foot, the endings of the shafts of the compound setae are like those of most other *Syllides* species (Fig. 4*f*, *g*); the 10–20 setae have blades with approximately the same form as anteriorly, and 15–60 μ length (25–35 μ in other specimens). Bundles of swimming setae start on the eighth (the holotype and 4 specimens) or ninth (1 specimen) setiger. Sexual products are present from the eighth setiger.

Discussion — In contrast to Pettibone (1963), this species is not considered here as a synonym of *S. setosa* because Verrill (1882), while describing the latter species, distinguished a smaller form, with smaller palps and a dark stomach (as here), but with swimming setae from the 10th body segment, from *S. setosa*. Moore (1908 p. 451), while describing *S. verrilli*, stated: "This is the species referred to by Verrill as having been taken at Woods Hole along with *S. setosa*" without further elaboration. In support of Pettibone's view, it can be noted that Verrill's fig. 11b and c (in Hartman 1944 pl. 56) of *S. setosa* show subapical spines at the shaft endings of the compound setae, an uncommon feature that is found only in *S. verrilli* and *S. convoluta* among the species that I have seen. However, even with a magnification lower than needed to recognize these spines, Verrill could not have overlooked the characteristic simple dorsal setae had they been present.

It is of some historic interest that the original labels of both types show that Moore first had intended to name this species for Webster.

Syllides japonica Imajima

Fig. 5

Syllides japonicus Imajima 1966 p. 112.
Syllides longocirrata. Pettibone 1963 p. 124.

Diagnosis — Large palps. Median dorsal cirri articulated. Pharynx sometimes with tooth. Proventricle through 4–6 segments. Single simple upper setae on all parapodia, long and pointed. Compound setae with pointed shaft endings throughout; blades bidentate, varying in length within median parapodia by a factor of 5; long and medium-sized blades with several spines at bases.

Material studied — Cape Cod Bay, Mass. (cf. Pettibone 1963 p. 125). A well preserved anterior fragment of a mature specimen, originally identified by Verrill as *S. setosa* (USNM 10080). New record.

Cape Cod Bay, near Manomet Buoy (6A), 25 m, sandy mud, July 8, 1954 (M. H. Pettibone coll., originally identified as *S. longocirrata*). USNM 33152 (one specimen). New record.

Harney Pass, Lopez Island, Wash., approximately 48°35.5′N, 122°55′W, 27 m, mud, July 1967 (H. L. Sanders coll.). Three well-preserved anterior fragments with up to 21 setigers. One specimen in USNM 45264. New record.

Additions to the description — An anterior end from Harney Pass is depicted to show the broad partly fused palps and the end of the pharynx (Fig. 5*a*). The soft papillae of the pharynx described by Imajima (1966) cannot be seen in any of the three specimens, which all had their pharynges everted. Further, a large *Syllis*-tooth as found by Imajima is definitely absent. The proventricle extends through 6 setigers rather than 4 or 5 as in the Japanese material. The aciculae (1, very rarely 2, per foot) are slightly expanded at the tips (Fig. 5*b*). The single upper simple setae are drawn out into fine tips and are slightly serrated. The compound setae number up to 20 per parapodium anteriorly and almost

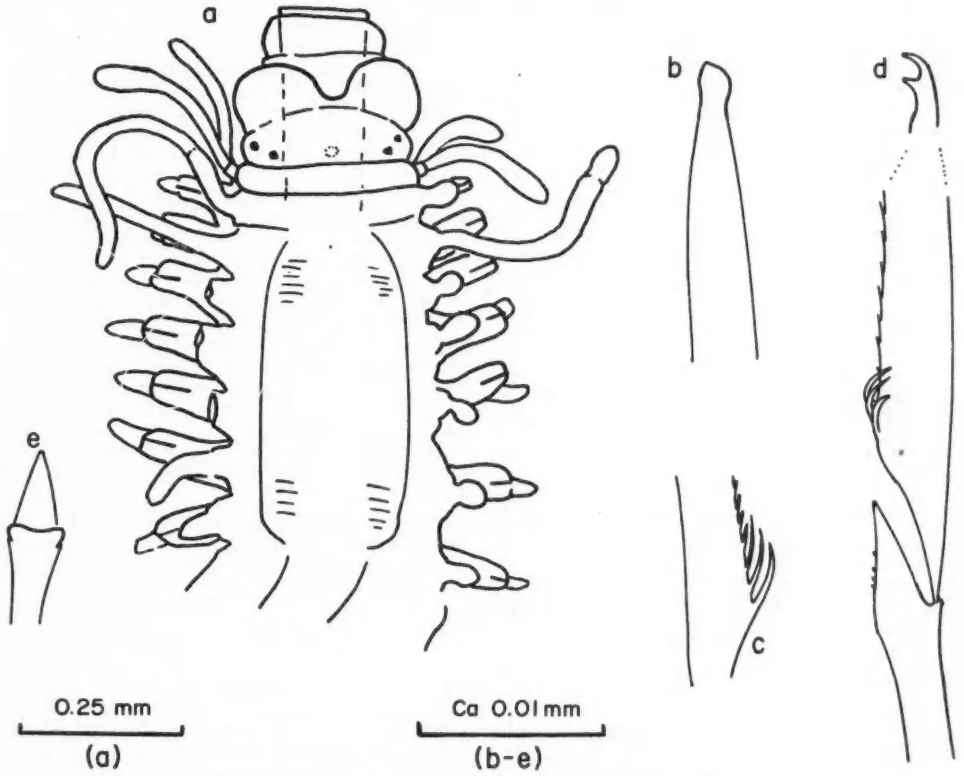

FIG. 5. *Syllides japonica* (*a–c* from Lopez Island, *d–e* from Cape Cod): (*a*) anterior end, dorsal view, setae omitted; (*b*) tip of acicula from 15th parapodium; (*c*) basis of blade of about 50 μ length from this parapodium, enlarged; (*d*) compound seta with blade of 150 μ length from 25th setiger; (*e*) end of shaft of compound seta in plane view.

10 in the region of the 20th setiger. The longest blades of the compound setae measure 125 μ and thus are 5 times as long as the shortest blades in the same parapodia. The basal spines (Fig. 5*c*) are sometimes reduced on the long blades.

The mature pelagic specimen from Cape Cod (cf. Pettibone 1963 fig. 36b p. 125) is approximately 3.5 mm long and at the end of the fragment (25th setiger) about 0.5 mm wide (without parapodia); a pharyngal tooth is not present. The parapodia are very long, as in Verrill's figure (pl. 56 fig. 11 in Hartman 1944) of *S. setosa*. They insert slightly beyond the middle of the parapodium and reach a little beyond the tips of the parapodia.

Single upper simple setae, present from the first setiger, are slightly flattened so that they appear almost whiplike, and carry small hairs on one edge. The compound setae were observed on the fourth and 25th setigers. The distal ends of the shafts are pointed throughout; all blades have bidentate tips (Fig. 5*d*). On the fourth setiger, 3 or 4 setae with blades 100–110 μ long and half a dozen each of setae with blades about 60 μ and 40–50 μ length are found. The blades of the uppermost setae studied on the 25th setiger are 110–150 μ long and have basal spines (Fig. 5*c*); medium-long blades of 80 μ length on this parapodium sometimes also have basal spines. The spines are absent on the corresponding setae of the fourth setiger; however, the proximal hairs on the cutting edges are more distinct than the distal ones. On the fourth and 25th parapodia, the short blades have conspicuous hairs proximally but are almost smooth distally. Bundles of swimming setae up to 1 mm long start on the 10th setiger.

The almost 4-mm long benthic specimen from Cape Cod (USNM 33152) is without swimming setae but otherwise agrees with the pelagic animal from the area.

Remarks — Verrill's specimen from Cape Cod is not considered to be *S. setosa* primarily because of the absence of subapical spines on the shaft endings of the compound setae. Also, the swimming setae start on the 10th setiger rather than on the eighth as in Verrill's original description.

Syllides benedicti n.sp.

Fig. 6

Syllides convoluta — Webster and Benedict 1887 p. 717.

Types — Holotype: USNM No. 384 from Eastport, Maine, intertidal sand, collected by Webster in 1880. A mounted, complete, and well preserved but very coiled specimen with somewhat more than 60 setigers and approximately 6.5 mm length.

Paratypes: Two smaller specimens on the slide with the holotype, four specimens on two other slides, and a vial with four specimens (USNM 45268), all apparently from the same site and year.

Diagnosis — Large palps. Median dorsal cirri articulated. Pharynx without tooth. Proventricle through 5–8 segments. Single simple upper setae on all feet, of similar width; in large specimens each with a tip with conspicuous irregular spines. Compound setae with pointed shaft endings throughout. Blades bidentate, without hairs on cutting edges, length varying by a factor of almost 5 within median parapodia; medium-size blades sometimes with basal spurs.

The name refers to the co-author of the publication giving the first record (Webster and Benedict 1887).

Material studied — Type series.

Skagerrak, sta. 149 of NMG, in the Grebbestad-Fjällbacka area, on the east side of Morö, Bohuslän, Sweden, 9.5 m, shell sand, *Zostera*, June 19, 1935 (L. A. Jägerskiöld coll., sta. 30 of *Skandia;* originally identified as *S. longocirrata* by A. Eliason). One anterior fragment, NMG Polych. 11396.

Description — The complete specimens have up to 70 segments, are up to 6.5 mm long and 0.3–0.4 mm wide (without parapodia). The width is possibly affected by pressure of the cover slip. The smallest animal, an anterior fragment with 29 setigers, is 2.7 mm long.

The palps are large and divergent (Fig. 6*a*). All mounted specimens have two conspicuous pairs of eyes, and some have an additional anterior pair of minute eye spots; eyes could not be well seen on the unmounted specimen. The antennae are rather clearly annulated (pseudo-annulated). The tentacular segment is distinct. The dorsal cirri are genuinely articulated (often with a smooth proximal quarter) from the third setiger and have a dozen or more articles, each being approximately twice as long as wide. The ventral cirri are short anteriorly (resembling Fig. 1*b* of *S. longocirrata*) and become gradually longer (cf. Fig. 6*k*) within the first 10 setigers, but do not change their places of insertion. The pygidium bears a small unpaired cirrus but the paired ones are lost.

A pharyngeal tooth is absent. In the smallest specimen, the pharynx (withdrawn) extends through 4 or 5 segments and the proventricle lies in 5–8 setigers. In the larger animals, the length of the pharynx is equal to that of 3 or 4 segments, but that of the proventricle equals 6–8 segments. The proventricle has 60–65 rows of muscular columns.

The tips of the aciculae (one per parapodium) are very slightly enlarged (Fig. 6*b*). Single upper simple setae are present from the first parapodium; the diameter is the same as that of the shaft of the compound setae. The convex stems are slightly serrated. In smaller animals, the tips are simply rounded, or appear as in Fig. 6*c*. The tips in the mounted large specimens sometimes bear irregular spines (Fig. 6*d*); occasionally the spines are connected by a membrane.

The number, approximately 7–10, of compound setae is similar on anterior and median setigers. The distal endings of the shafts are uniform throughout the body. In side view they are characterized by a fairly abrupt widening and vary between the shape depicted in Fig. 6*e* and that in Fig. 6*f*. In plane view, they are sharp and pointed (Fig. 6*g*). The length of the blades ranges bet-

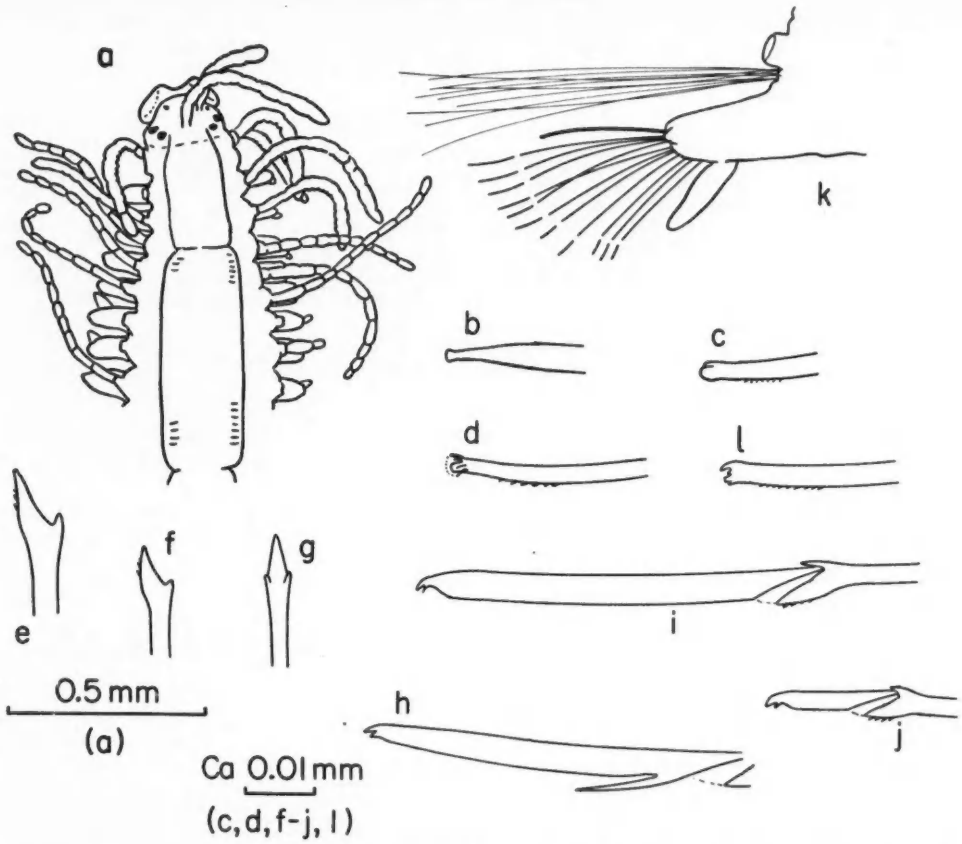

FIG. 6. *Syllides benedicti* n.sp. (*a–h* from type series; *i–l* from NMG Polych. 11396): (*a*) dorsal view of anterior end, slightly squeezed; left antenna and ventral tentacular cirrus missing, setae omitted; (*b*) end of acicula; (*c, d*) upper simple setae; (*e, f*) ends of shafts of compound setae in side view; (*g*) end of shaft of compound seta in plane view; (*h*) compound setae with medium-long blade; (*i, j*) blades of compound setae; (*k*) 15th foot; (*l*) upper simple seta.

ween 15 and 70 μ within median feet. The length of the longest blades does not change much throughout the body, the longest blades on the fifth foot being 50 μ long. Hairs on the cutting edges are absent. The blades of intermediate length have a basal spur (Fig. 6*h*). In the type material, the tips of the blades are probably bidendate, although this character could only be clearly seen on a few setae.

The well-preserved anterior fragment with 13 setigers from the Skagerrak can be referred to this species, although it differs somewhat from the typical form. The ends of the dorsal simple setae in the neuropods are very variably shaped (for example, Fig. 6*l*). The number of compound setae is greater (approximately 15–18 per foot) on all feet, the ends of their shafts are more strongly serrated (Fig. 6*i, j*), and the width of the blades is constricted proximal to the secondary tooth. Also, on 3 dissected feet, the basal spur was recognized only on 2 intermediate-size blades. The longest blades of the compound setae (6–8) are 70–80 μ long; the shortest blades (2–6 setae) are 20 μ long; there are also 4–6 medium-size blades. Bundles of swimming setae occur from the 10th setiger (Fig. 6*k*) and one embryo had been attached ventrally on each side on the 13th setiger, and possibly also on the 12th.

Remarks — As implied, I do not accept the view by Webster and Benedict (1887) that the present material is identical with *S. convoluta* from Provincetown, Mass., the type locality, except for the difference in size.

Key for *Syllides*

The *Syllides* species regarded as valid in Hartman (1959, 1965), excepting *S. setosa*, and those treated here, can be distinguished as follows.

1. With papillated epidermis ..... *S. papillosa*
   With smooth epidermis 2
2. With smooth dorsal cirri on median segments. Conspicuous palps (sometimes folded beneath prostomium) 3
   With articulated dorsal cirri on median segments 5
3. Antennae and dorsal cirri bottle-shaped. Pharynx through 4 segments ..... *S. liouvillei*
   Antennae and dorsal cirri club-shaped. Pharynx through 1 segment 4
4. Setigers 12. Proventricle through 2 segments. Simple seta only posteriorly ..... *S. edentula*
   Setigers more than 12. Proventricle through 3 segments. Upper simple setae from first setiger ..... *S. sexoculata*
5. Shaft endings of compound setae on anterior segments very different from those on median and posterior segments (cf. Figs. 1*h*, 4*d*). Palps large or minute 6
   Shaft endings of all compound setae similar. Palps large 7
6. Upper simple setae conspicuously thick and bent on first 5 setigers (Fig. 1*f*), long and drawn out posteriorly. Blades of anterior compound setae serrated as in Fig. 1*h*, *i*. Palps large .. *S. longocirrata*
   Upper simple setae similar on all parapodia, with bifurcated tips (Fig. 4*b*). Blades of anterior compound setae as in Fig. 4*d*. Palps as minute papillae ..... *S. verrilli*
7. Shaft endings of compound setae with large subapical spines opposite sockets of blades (Fig. 3*c*). Upper simple setae with split tips (Fig. 3*b*) ..... *S. convoluta*
   Shaft endings of compound setae smooth or slightly serrated (Fig. 2*f*) 8
8. Some blades of compound setae on median parapodia with basal spurs (Fig. 6*h*) or large spines (Fig. 5*c*) 9
   Blades on median parapodia smooth or with hairs on cutting edges 10
9. Medium-long blades with basal spurs (Fig. 6*h*). Upper simple setae with terminal, irregular spines (Fig. 6*d*) ..... *S. benedicti*
   Long and medium-long blades each with several basal spines (Fig. 5*c*). Upper simple setae drawn out and pointed ..... *S. japonica*
10. Upper simple setae with rounded tips (Fig. 2*d*) ..... *S. fulva*
    Upper simple setae drawn-out and pointed 11
11. Proventricle through 4 setigers; blades of upper compound setae about 20 times as long as they are wide ..... *S. kerguelensis*
    Proventricle through 6–10 setigers; upper compound setae with very long blades, anteriorly >0.2 mm ..... *S. articulosa*

Remarks — It is to be noted that Monro (1939, under *Grubea rhopalophora* Ehlers) wrote about *Syllides kerguelensis* (McIntosh), "The bristles are very like those of *Syllides articulosus*" whereas they are rather short in McIntosh (1885 pl. 15A fig. 12). A new study of McIntosh's species is desirable. Also, from the rejected records, especially of *S. longocirrata*, it is obvious that several additional species, yet to be described, have already been collected.

Little can be said about the relation of the known species to each other. Obviously, *S. longocirrata* is the most specialized (derived) form on account of the anterior compound setae and their shafts, and the differentiation of the upper simple setae. Closely related is *S. verrilli* with similarly formed distal endings of the shafts of the compound setae on anterior setigers. Another specialized feature in the genus may be that the same basal spur on the blades of some setae occur in *S. longocirrata* and *S. benedicti*. However, whether one considers, among the remaining species, those with smooth dorsal cirri as more primitive than those with articulated cirri, or vice versa, depends on which is to be viewed as primitive among the Eusyllinae.

Acknowledgments

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Schroederella berkeleyi sp.n., un nouvel Orbiniidé (Polychète Sédentaire) de la faune interstitielle littorale du Massachusetts (USA)[1]

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LAUBIER, L. 1971. *Schroederella berkeleyi* sp.n., un nouvel Orbiniidé (Polychète Sédentaire) de la faune interstitielle littorale du Massachusetts (USA). J. Fish. Res. Bd. Canada 28: 1483–1486.

L'auteur décrit une nouvelle espèce d'annélides polychètes Orbiniidae du genre *Schroederella*, et la compare à l'unique espèce antérieurement connue, *S. pauliani*. Comme le générotype, *S. berkeleyi* sp.n. habite le domaine interstitiel littoral, et s'en distingue du double point de vue morphologique et biogéographique.

LAUBIER, L. 1971. *Schroederella berkeleyi* sp.n., un nouvel Orbiniidé (Polychète Sédentaire) de la faune interstitielle littorale du Massachusetts (USA). J. Fish. Res. Bd. Canada 28: 1483–1486.

The author describes a new species of polychaetous annelid belonging to the genus *Schroederella* (Orbiniidae), and compares it to the only previously known species, *S. pauliani*. Like the type-species, *S. berkeleyi* sp.n. lives in the littoral interstitial biotope, and is distinguishable from it by both morphological and biogeographical arguments.

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PARMI les annélides polychètes adaptées à la vie dans le domaine interstitiel littoral (mesopsammon de Remane et Schulz 1934), la famille des Orbiniidae Hartman 1942 (=Ariciidae Audouin et Milne Edwards 1833) ne comprenait jusqu'à présent qu'un seul genre strictement inféodé au milieu interstitiel, le genre *Schroederella* Laubier 1962, récolté dans les sables littoraux de Sandwich Bay, au Sud de Walvis Bay, en Afrique du Sud (Laubier 1962, 1967). Ce genre, créé pour renfermer l'unique espèce *Schroederella pauliani* Laubier 1962, est demeuré jusqu'à présent monotypique.

C'est donc avec un grand intérêt que j'ai recu une trentaine de Polychètes interstitielles récoltées sur les côtes du Massachusetts (USA) que le Dr M. Pettibone, qui avait reconnu leur appartenance au genre *Schroederella*, a bien voulu m'adresser pour étude. L'examen de ces spécimens a montré qu'ils différaient spécifiquement du générotype *Schroederella pauliani*, comme le laissait prévoir l'éloignement des deux localités. L'espèce nouvelle est sincèrement dédiée au Dr C. Berkeley.

Schroederella berkeleyi sp.n.

Fig. 1

Localité, types — Trente spécimens de *S. berkeleyi* sp.n. ont été récoltés dans les sables intertidaux de Craigville Beach à Centerville, Barnstable County, Massachusetts, par W. J. Wall, le 26 juin 1969. La zone de récolte est située dans une petite baie où débouche une rivière (Bumps River); la salinité de l'eau y varie entre 26‰ à marée basse et 31‰ à marée haute. Le sable est riche en particules organiques. Ce matériel a été déposé dans les collections de la Smithsonian Institution sous les numéros de catalogue 44946 pour l'holotype et 44947 pour les paratypes.

Taille, coloration — La longueur de *S. berkeleyi* sp.n. varie entre les deux valeurs extrêmes de 2.5 mm (individu de 22 segments) et 6.6 mm (individu de 40 segments). La valeur la plus fréquente est de 6 à 6.2 mm, avec un nombre total de segments compris entre 30 et 35. Des chiffres du même ordre ont été relevés chez *S. pauliani*. Toutefois, chez cette dernière espèce, des individus de plus petite taille avaient été récoltés: 1 mm de longueur pour 8 à 10 segments.

[1]Contribution no 51 du Groupe Scientifique du Centre Océanologique de Bretagne.

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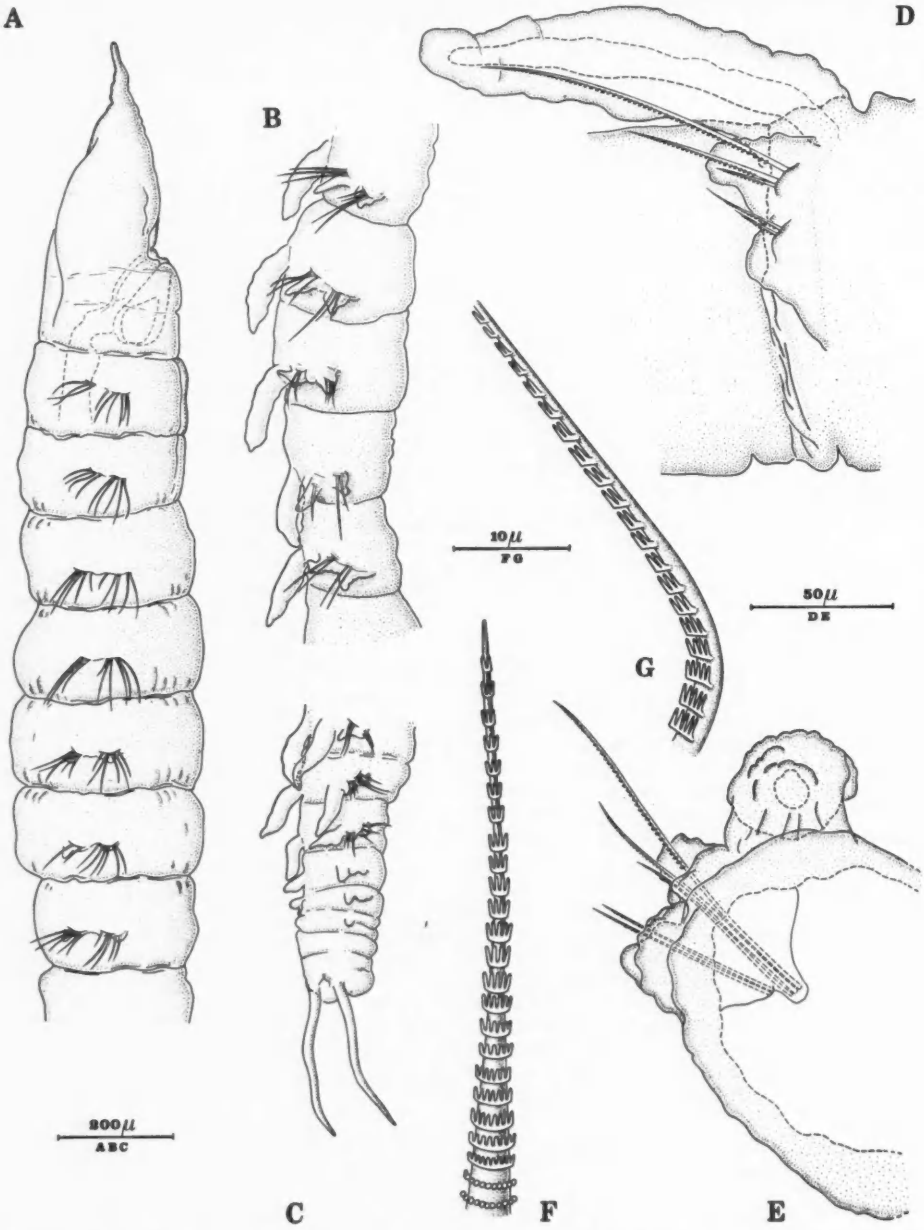

FIG. 1. *Schroederella berkeleyi* sp.n. holotype: A, partie antérieure; B, région abdominale, du 24ème au 28ème segment; C, région abdominale, du 30ème segment au pygidium; D, 28ème segment en vue latérale; E, le même vu de face; F, soie à plaquettes crénelées de face; G, la même de profil.

Dans l'alcool, les animaux sont blanchâtres; seules sont visibles les deux taches rouge vermillon des yeux. Une dépigmentation semblable avait été observée chez *S. pauliani*; elle est probablement en relation avec le mode de vie de ces animaux.

Prostomium — Le prostomium de *S. berkeleyi* sp.n. est semblable à celui de *S. pauliani*. Le prolongement antérieur régulièrement effilé est une caractéristique générique, en même temps qu'une remarquable adaptation à la vie dans le domaine interstitiel. Cependant, l'articulation entre la pointe et la partie postérieure du prostomium est moins marquée que chez *S. pauliani*. Les deux yeux rouge vermillon sont profondément enfoncés dans les téguments, et les organes nucaux décrits chez *S. pauliani* ne sont pas visibles chez *S. berkeleyi* sp.n.

Corps — Le corps est divisé en deux régions, une région thoracique abranche et une région abdominale branchifère. La transition entre ces deux parties est progressive, la branchie apparaissant d'abord sous la forme d'une protubérance hémisphérique, puis d'un prolongement de plus en plus long à extrémité arrondie. Cette zone de transition compte 3 à 5 segments. La première branchie (c'est-à-dire au début de cette zone de transition) apparaît au 14–15ème segment (soit le 12e–13e sétigère) chez les animaux de grande taille, au 11e segment (soit le 9e sétigère) chez le plus petit individu.

Le segment buccal est moins distinct que chez *S. pauliani*. Cependant, il existe bien deux segments achètes en arrière du prostomium, comme le laisse supposer la longueur de l'ensemble compris entre ce dernier et le premier segment sétigère: on distingue une très fine ligne intersegmentaire.

Région thoracique — Les parapodes de cette région présents à partir du 3ème segment comprennent deux rames, un notopode et un neuropode. Les lobes postérieurs apparaissent à la rame dorsale au 7ème segment, sous forme d'un simple bouton qui s'accroît ensuite sur les segments postérieurs pour former un prolongement digitiforme. A la rame ventrale, il n'y a pas de lobe postérieur, mais seulement un mamelon sétigère qui devient bien visible à partir du 7ème segment également.

Dans la région thoracique, les soies sont toutes semblables. Ce sont des soies capillaires à plaquettes crénelées, identiques à celles décrites chez *S. pauliani*. Ces plaquettes sont constituées par des anneaux incomplets insérés à peu près perpendiculairement au corps de la soie et porteurs d'une série de 12 à 2 fines dents parallèles à l'axe de la soie, le nombre de dents décroissant de la base vers la pointe de la soie. Cette structure, délicate à observer, est semblable à celle décrite chez *S. pauliani*. Le nombre de soies à plaquettes crénelées décroît d'avant en arrière: de 8 à 9 soies à chacune des deux rames des segments les plus antérieurs, à 2 à 3 soies dans les derniers segments antépygidiaux.

Chaque rame est soutenue par un (parfois deux) acicule pointu. Contrairement à ce qui se passe chez *S. pauliani*, il n'y a jamais d'uncini sur les neuropodes de la région thoracique. A elle seule, cette différence justifie la création de l'espèce nouvelle *S. berkeleyi*.

Région abdominale — Cette région est essentiellement caractérisée par l'apparition des branchies. Les branchies, en position latéro-dorsale, sont constituées par un simple filament inséré au niveau du parapode, recourbé vers l'arrière et prenant très tôt une direction à peu près parallèle à l'axe longitudinal du corps. Dans la région abdominale, le lobe dorsal est bien développé, et représente environ le cinquième de la longueur de la branchie. Il n'y a pas de véritable lobe postsétal au neuropode, mais un simple mamelon sétigère. Aux deux rames, les soies capillaires à plaquettes crénelées sont toujours présentes, parfois accompagnées aux notopodes d'une soie capillaire lisse en aiguille, plus fine que les soies à plaquettes. Il n'y a pas d'uncini dans la région abdominale, pas plus que dans la région thoracique. Chaque rame est soutenue par un acicule en aiguille. Enfin, on distingue parfois de très petites soies capillaires, qui semblent bien, d'après leur ornementation, n'être que des soies à plaquettes en formation.

Les trois à quatre derniers segments antépygidiaux sont dépourvus de soies, on distingue simplement les ébauches des branchies et des parapodes.

Pygidium — L'anus s'ouvre dorsalement, entre les bases de deux longs et grêles cirres latéro-dorsaux. Ventralement, le pygidium porte deux lobes trapus et grossièrement arrondis. A la longueur des cirres latéro-dorsaux près, tout ceci est semblable au pygidium de *S. pauliani*.

Justification

Sur le plan morphologique, les différences entre *S. pauliani* et *S. berkeleyi* sp.n., bien que peu nombreuses, paraissent suffisamment importantes pour justifier la création d'une espèce nouvelle pour la forme américaine. *S. berkeleyi* sp.n. se distingue du générotype par l'absence complète d'uncini, la longueur exceptionnelle des cirres pygidiaux latéro-dorsaux, la segmentation peu marquée entre prostomium et premier segment et premier et second segments, enfin l'articulation indistincte de la partie antérieure du prostomium avec la base. En plus de ces critères morphologiques, la répartition des deux espèces apporte un élément important du point de vue biogéographique, même si l'on tient compte du cosmopolitisme relatif (c'est-à-dire considéré par rapport aux formes voisines non interstitielles) des animaux peuplant les sables intertidaux: *S. pauliani*, décrite de la région de Walvis Bay (Sud-Est Atlantique), n'a jamais été retrouvée depuis sa découverte (Day 1967), et *S. berkeleyi* sp.n. a été recueillie sur les

côtes du Massachusetts (Nord-Ouest Atlantique).

Depuis la création du genre *Schroederella*, la sous-famille des Protoariciinae Hartman 1957 s'est enrichie de deux genres nouveaux non interstitiels, *Protoariciella* Hartmann-Schröder 1962 et *Scoloplella* Day 1963. Le prostomium normalement arrondi de ces deux genres, les biotopes respectifs des trois espèces qu'ils comprennent actuellement, bien différents des sables intertidaux, confirment la validité du genre *Schroederella*.

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Bioluminescence in Pelagic Polychaetes

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DALES, R. P. 1971. Bioluminescence in pelagic polychaetes. J. Fish. Res. Bd. Canada 28: 1487–1489.

Of six holopelagic polychaete families, the Tomopteridae and Alciopidae are the only ones having representatives that appear to be photogenic. Previous investigators localized the site of photogenic organs to certain parapodial glands in the tomopterids. Photogenic organs have not been demonstrated in the alciopids, but some species have been reported with little substantiation to be luminescent. The structure and function of the photogenic organs and the nature of the luminescent products are incompletely known, exemplifying gaps in the knowledge of the anatomy and life history of pelagic polychaetes.

DALES, R. P. 1971. Bioluminescence in pelagic polychaetes. J. Fish. Res. Bd. Canada 28: 1487–1489.

Seuls parmi six familles de polychètes holopélagiques, les Tomopteridae et les Alciopidae ont des représentants qui semblent photogènes. D'autres chercheurs ont déjà localisé, sur certaines glandes du parapode, l'emplacement des organes photogènes des tomoptéridés. On n'a pas trouvé d'organes photogènes chez les alciopidés, mais on a attribué la luminescence à certaines espèces sans trop de justification. Les structures et fonction des organes photogènes et la nature des produits luminescents ne sont que partiellement connues, preuve des lacunes qui existent dans nos connaissances de l'anatomie et du cycle vital des polychètes pélagiques.

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MANY holopelagic polychaetes live at depths below the photic zone. None of the Typhloscolecidae, Lopadorhynchidae, Iospilidae, or Pontodoridae have obvious photogenic organs. Furthermore, their eyes are reduced or absent. Of the remaining families, the Tomopteridae do have organs described as photogenic, whereas the Alciopidae are described as luminescent, although in them photogenic organs have not been identified. Tomopterids have rather small eyes; alciopids have eyes that are notable for their large size and spherical lenses. Clark (1970), in describing the extraordinarily well-developed mucus glands in the alciopid *Rhynchonerella angelini* (Kinberg), suggests that these glands might excrete a luminescent material. This is an interesting speculation and serves to emphasise how little we know about the anatomy and way of life of these organisms. The purpose of this note is to review briefly what is known.

Greeff (1882, 1885) was the first to record that a *Tomopteris* was luminescent, noting in *Tomopteris mariana* Greeff that it was the parapodia that were luminescent and localizing the site of production to the rosette organs. The rosette organs, which have a nerve supply, are derived from coelomostomes, as Meyer (1926, 1930) later demonstrated in *Tomopteris helgolandica*. Malaquin and Carin (1922) stressed that tomopterids without rosettes had hyaline glands and that the two organs were homologous. Both are distinguishible from other secretory glands in the parapodia by their position and by the nature of the secretory material they produce, which appears to be lipid. More recently, Terio (1960, 1964) has described both male and female *Tomopteris septentrionalis* Steenstrup with mature gametes as having secretory material, suggesting lipofuscin in the hyaline glands, which has an emission spectrum with broad bands around 500–600 nm (max 560–580 nm) and a narrower band around 490 nm (Terio 1960).

Terio (1964) has examined *Tomopteris nationalis* Apstein with a Leitz fluorescence microscope, and has described channels radiating from the rosette organs situated near the tips of the parapodial rami through the pinnae and opening along the edges, suggesting that the product is expelled. Here the emission spectrum had a maximum between 500 and 600 nm with another peak around 404 nm.

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Viewed with ultraviolet light, the central pigment of the rosette organs appears orange and the channels radiating to the edges of the pinnules fluoresce yellow or greenish yellow. Nothing more is known, either about the substances themselves or of their production. Terio's work tends to confirm the suggestion that it is the rosettes or the hyaline glands, as the case may be, that are the photogenic organs. Their occurrence and distribution varies from one species to another and could, if light were generated simultaneously in all of them, produce different species-specific patterns that might act as recognition signals for pairing. Beyond Greeff's original observations and those of Terio we do not know what the other parapodial glands are for. Harvey (1952), while at the Plymouth Laboratory, observed that *Tomopteris helgolandica* produced "a yellowish light" and that extracts gave no light with *Cypridina* luciferin solution; but other references to luminescence in tomopterids in the literature are all quotations of these few original observations (Kiernik 1908; Lo Bianco 1909).

Harvey (1952), while stating that the alciopids *Corynocephalus* (?*Alciopina*), *Callizonella* (?*Krohnia*), and ?*Rhynchonerella* are luminescent, does not quote any authority. Lo Bianco (1909) suggests that the pigmented parapodial gland in *Krohnia* (*Callizonella*) *lepidota*, which he states is absent in the female, could be a photogenic organ, but as Clark (1970) notes, there is no evidence for this suggestion. Clark (1970), in his paper on *Rhynchonerella angelini*, makes no claim that the epidermal mucus glands, which have in this alciopid been invaded by the nervous system in such a spectacular fashion, are photogenic, only speculating they might be. His original specimens, collected by attraction to a light at Friday Harbor, Washington, were not noticed to luminesce when they were collected. He described the cells as containing an acid mucopolysaccharide material that was PAS-positive and stained intensely with paraldehyde fuchsin and alcian blue. Such reactions are certainly unlike the substances in the rosettes and hyaline glands in the tomopterids described by Terio, although other polychaetes such as *Chaetopterus* do produce a luminescent "mucus." Bonhomme (1954), surveying the variety of luminescent polychaetes, concluded that, in general, "errant" worms produced luminous flashes, the light being produced intracellularly by photocytes, whereas, in the luminescent "Sedentaria," the light is produced in a secreted mucus. His own histological investigations of material fixed in Flemming's mixture, however, led him to suggest that in *Tomopteris kefersteini* Rosa the photogenic cells produce osmiophilic granules representing the photogenic material that is excreted. This concurs with Terio's conclusions. The only one who seems to have actually seen an alciopid luminesce is Okada who, in 1925 wrote "In the evening of August 25, 1919, the writer, while engaged in examining the dredgings from the bottom of the Sagami Sea at a depth of about one thousand meters, observed a large specimen of *Crateromorpha meyeri* Gray to be brightly luminous. The whole body of the sponge glowed for several hours after being brought into a dark room. The luminescence consisted of a thousand spots of a blue light resembling the stars in the sky. On dipping the sponge into fresh water the light shone particularly brightly but at the same time the luminous spots were observed to be transferred from the body of the sponge into the surrounding medium. Each spot proved to be a small annelid belonging to the family Alciopidae."

The eyes of *Tomopteris helgolandica* have been studied recently by Åkesson (1964), following Nänni (1911) and Hachfield (1926), and he has compared these with the eyes of alciopids studied many years before by Andrews (1892), Béraneck (1893), and Demoll (1909). Åkesson emphasises the differences in *Tomopteris* from that of alciopids; indeed the *Tomopteris* eye appears to be very different in structure from those of all other polychaetes. Both tomopterids and alciopids are carnivorous animals and both have an eversible proboscis. Some alciopids live near the surface, but others with equally large eyes live well below the photic zone. The development of the eyes suggests that these worms detect their prey by sight (Dales 1955). The lenses, at least in some, are red and spherical, and would serve to focus the mainly blue light at the lower limit of the photic zone, or the light emitted by organisms on which they may feed. It would seem that we know very little, and one can but hope that where living pelagic polychaetes can be collected and studied in the laboratory, any opportunity will be taken to learn more about these animals. Clark's (1970) *Rhynchonerella angelini* were collected at Friday Harbor, Washington, but this species is perhaps the least removed from the phyllodocids from which the alciopids must have been derived. Incidentally, one of the earliest reports of luminescent worms was that of Potts (1913) of *Odontosyllis* in the waters around Nanaimo, B.C.

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Two New Records of Benthic Polychaetes from Washington[1]

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NICHOLS, F. H. 1971. Two new records of benthic polychaetes from Washington. J. Fish. Res. Bd. Canada 28: 1491–1492.

Two benthic polychaete species, *Chloeia entypa* Chamberlin and *Drilonereis falcata minor* Hartman, heretofore not recorded from the northeast Pacific Ocean, have been found in samples from the Washington coast, Juan de Fuca Strait, and Puget Sound. These new records reflect incomplete knowledge of the polychaete fauna of these areas.

NICHOLS, F. H. 1971. Two new records of benthic polychaetes from Washington. J. Fish. Res. Bd. Canada 28: 1491–1492.

On a trouvé dans des échantillons provenant de la côte de Washington et des détroits de Juan de Fuca et de Puget deux espèces de polychètes benthiques, *Chloeia entypa* Chamberlin et *Drilonereis falcata minor* Hartman, jusqu'ici inconnues du Pacifique Nord-Oriental. Ces nouvelles mentions témoignent des connaissances fragmentaires qu'on a de la répartition des polychètes de ces régions.

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IN the benthic collections of K. D. Hobson, U. Lie, and the author, from Puget Sound, Juan de Fuca Strait, and off the Washington coast, are two species of polychaetes not previously known from the northeast Pacific Ocean. These new records probably reflect incomplete knowledge of the deepwater fauna of the area, and particularly of those species that, like the *Drilonereis* species described below, are very small and, consequently, are lost when the samples are washed through a screen or during sorting.

Family AMPHINOMIDAE

Chloeia entypa Chamberlin

Chloeia entypa Chamberlin 1919 p. 30; Hartman 1940 p. 205.

Material studied — Twenty-five miles off the coast of Washington (station 44: 46°40.0′N, 124°41.5′W, 180 m depth, fine sand, July 10, 1968, see Lie and Kisker 1970), five specimens.

Remarks — The specimens have proximally directed serrations on some posterior bifurcated notosetae. These same setae also have a prominent secondary fang. However, the single, reddish-brown dorsal stripe described by Hartman (1940) is not obvious in these specimens. Instead, the entire animal is so colored, possibly due to storage in 70% alcohol.

The species was previously known from central America, western Mexico, and California. Thus, this new record is an extension of its range.

Family ARABELLIDAE

Drilonereis falcata minor Hartman

Drilonereis falcata minor Hartman 1965 p. 123.

Material studied — Southern Puget Sound (station 6: 47°10.7′N, 124°04.8′W, 34 m depth, mixed mud, sand, gravel, May 2, 1963, see Lie 1968), two specimens. Port Madison, Washington (station E: 47°22.4′N, 124°26.3′W, 34 m depth, silty sand, October 21, 1965, see Nichols MS 1968), one specimen. Juan de Fuca Strait (station 2: 48°21.5′N, 124°04.8′W, 170 m depth, mud with gravel, June 12, 1965; station 3: 48°22.4′N, 124°26.3′W, 140 m depth, mud with gravel, June 12, 1965, O. O. Hobson unpublished data), five specimens.

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Remarks — This subspecies is distinguished from the typical form of the species *D. falcata*, and indeed from most *Drilonereis* species, in that the bases of maxillae I have only two or three large blunt teeth each, maxillae II have only two large teeth, maxillae III have only one tooth, and maxillae IV are absent. Hartman (1965) has designated *D. falcata minor* a subspecies primarily because of the similarities of the parapodia, setae, and acicular spines with those of *D. falcata*. But, because of the important differences between this subspecies and the typical form in the shape and number of maxillary pieces, this designation might be questioned. However, additional specimens of both forms must be found before a diagnosis can be made complete.

Hartman (1965) reports the occurrence of this subspecies in New England, and that of the typical form in California and South Africa.

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Simulation Studies of the Adams River Sockeye Salmon (*Oncorhynchus nerka*)

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LARKIN, P. A. 1971. Simulation studies of the Adams River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada 28: 1493–1502.

The pattern of abundance of sockeye salmon (*Oncorhynchus nerka*) of the Adams River since 1938 is: 1 year large or "dominant," 1 year small or "subdominant," and 2 years very small or "off." In recent years, the subdominant run has shown indications of becoming as large as the dominant. This pattern can be accounted for by a model system in which predation is not sufficient to influence the dominant run, but predators, benefited by the abundance of prey, remove such a large fraction in the 3 succeeding years that the pattern is retained. Buffering of predation by the dominant run accounts for the larger size of the subdominant. Patterns similar in form to those observed naturally since 1922 are produced over a narrow range of parameters, and suggest that the particular circumstances of the Adams run are necessary to the nature of the population fluctuation, but are not so particular that some other pattern could not have emerged with a different sequence of environmental conditions. Taking an array of results of a series of simulations suggests that the odds of developing the existing pattern were about 50:50, although the subdominant run would more commonly become dominant as well by 1951, rather than as late as the 1960's. The double dominance situation is stable in the model system. In the present circumstances it seems appropriate to explore the possible benefits of managing the fishery so as to enhance the growth in size of the subdominant run, and perhaps to consider predator-removal programs to enable development of large runs on all 4 years of the traditional cycle.

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Depuis 1938, l'abondance du saumon sockeye (*Oncorhynchus nerka*) de la rivière Adams présente le schéma suivant: une année d'abondance ou "dominante," une année de moindre abondance ou "sous-dominante" et deux années de rareté ou "mortes." Depuis quelques années, la montée sous-dominante paraît devenir aussi abondante que la dominante. Ce phénomène peut s'expliquer par un système modèle en vertu duquel la capture par les prédateurs n'est pas assez importante pour affecter la montée dominante, mais où les prédateurs, profitant de l'abondance des proies, prélèvent une forte portion des montées des trois années subséquentes, de sorte que le schéma demeure le même. L'action tampon de la montée dominante sur les prédateurs explique l'abondance de la montée sous-dominante. Des schémas analogues à ceux observés en nature depuis 1922 se rencontrent dans une étroite gamme de paramètres, ce qui donne à entendre que les particularités de la montée de la rivière Adams sont essentielles à la nature des fluctuations du stock, sans toutefois empêcher l'émergence d'un schéma différent devant une séquence de conditions ambiantes différente. L'alignement des résultats d'une série de simulations suggère que les chances d'obtenir le schéma actuel sont d'environ 50:50. La montée sous-dominante aurait cependant eu, en général, plus de chance de devenir dominante avant 1951 que plus tard durant les années 60. Cette situation de double dominance est stable dans le modèle. Dans les circonstances, il serait bon d'étudier les bénéfices possibles d'un aménagement visant à accroître la montée sous-dominante, et peut-être songer à des programmes d'élimination des prédateurs en vue de favoriser d'abondantes montées au cours des quatre années du cycle traditionnel.

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THE historical pattern of fluctuation in abundance of the Adams River population of sockeye salmon (*Oncorhynchus nerka* Walbaum) has been the subject of considerable speculation. Ricker (1950) suggested that natural predation has potential as a causative mechanism for the cyclical pattern of a large run (the dominant), a moderate run (the subdominant), and two very small runs (the off years). After considering and discarding a number of alternative hypotheses, Ward and Larkin (1964) developed the predation theory, using a simulation model that demonstrated quantitatively that predation mechanisms could produce the observed pattern of fluctuation. Briefly, the model was based on the idea that predation is not sufficient to influence the dominant run, but that predators, benefiting from the dominant run, remove such a large fraction in the other 3 years of the cycle that the dominance pattern is retained. The model incorporates the added feature that smolts of the large run "buffer" predation on fry of the year following, and this results in the development of a subdominant run. Regardless of the probable inaccuracy of these assumptions (the natural system being much more complex) the model produced simulations that resembled remarkably the natural events since 1922, with the notable exception that the subdominant run in the simulations commonly assumed equal status with the dominant whenever the subdominant reached levels comparable to those observed naturally. This was taken to mean that the model was inadequate, but recent natural events (Table 1) suggest the possibility that the subdominant run *is* becoming abundant, and have therefore prompted this present analysis. Table 1 gives the spawning populations for 1938–69, which are usually from one-fifth to one-third of the total run for a year. The spawning population in 1970 was 2 million fish.

Using the model described in Ward and Larkin (1964), and running simulations with the general salmon simulator of Larkin and Hourston (1964), the following questions were asked:

(1) How sensitive is the model system to variations in parameters? The model system is capable of generating a very wide range of kinds of population fluctuation. If the natural Adams River pattern is commonly imitated in simulations for a group of parameter values that could describe any of several sockeye populations, then the usefulness of the model in describing the Adams case seems dubious, for the Adams pattern is quite unusual. Alternatively, if the natural pattern occurs over a very narrow range of parameters (particularly for the random climate factors), and then only seldom, it would imply that either the natural system is largely fortuitous, or that the structure of the model had been inadvertently contrived to describe what *has* happened and has no usefulness in predicting. Ideally, the model should produce an appropriate type of pattern of fluctuation over a fairly narrow range of parameters, but should also suggest that the course of natural events has in part been fortuitously determined by climatic factors.

(2) If the model demonstrates the appropriate characteristics of sensitivity, as to give confidence in its predictive capabilities, what would one expect to happen in the next few years in the natural system?

TABLE 1. Annual estimated spawning populations of Adams River sockeye, 1938–69.

Cycle I (dominant)		II (subdominant)		III		IV	
Year	No. spawners	Year	No. spawners	Year	No. spawners	Year	No. spawners[a]
1938	776000	1939	32000	1940	12000	1941	50
1942	2568000	1943	10000[b]	1944	2000	1945	67000
1946	2352000	1947	200000	1948	15000	1949	22000
1950	1268000	1951	145000	1952	11000	1953	222000
1954	2066000	1955	64000	1956	8000	1957	307000
1958	2274000	1959	135000	1960	2000	1961	66000
1962	1151000	1963	157000	1964	800	1965	58000
1966	1285000	1967	840000	1968	4000	1969	53000

[a]In cycle year IV, over 95% of the spawners were 3-year-old males (jacks).

[b]The 1943 estimated population seems too small to have produced the 1947 populations. It is possible that this estimate is in error. There may also have been an unusually large production of 5-year-olds by the 1942 spawning.

The Model System and the Sensitivity Simulations Conducted

The steps in the life history of each year-class in the model for simulating the Adams River sockeye population fluctuation, and the values used for various parameters, were as follows:

(1) *Spawning population* — The population of spawners each year (w_t) comprises the sum of fixed proportions of the productions from appropriate years previous, i.e.,

$$w_t = \sum_{i=k}^{i=l} p_{ij} Z_{t-i}, \qquad (1)$$

where p_{ij} are the proportions of fish that spawn at each age i for each cycle year, j, and Z_{t-i} are the productions of recruits that survive to become adults and that contribute to the spawning population in year t as fish of ages l to k. This technique of forming the spawning population follows that of Ward and Larkin (1964). Each spawning population comprises individuals born various numbers of years previously, and age of return was treated as a cycle characteristic, all the simulations using the averaged observed Adams age distributions of production from various cycle years, as given by Ward and Larkin (1964), i.e.,

	Proportion of progeny maturing at age		
Cycle	3	4	5
I	.0912	.9076	.0022
II	.0735	.9181	.0084
III	.1065	.8710	.0225
IV	.3040	.6960	.0000

This procedure is not inconsistent with the natural situation, for there is no evidence to suggest for the Adams that the proportion of fish that mature at various ages is influenced by density (Ward and Larkin 1964).

In calculating the spawning stock, the proportions of 3-year-olds were multiplied by 0.02 to take account of the great preponderance of males and the relatively small numbers of eggs contributed by each female.

(2) *Compensation stage* — The production of fry from each year's run (t) conformed to the relation

$$Z_1 = w_t e^{a_1(1-w_t)}, \quad Z \leq 1$$

$$Z_1 = (1-D)e^{-a_2(w_t-1)} + D, \quad Z > 1 \qquad (2)$$

where a_1, the compensation coefficient for the Adams, has historically been about 2.0. In the simulations it was also used at 1.5 and 2.5. The coefficient D sets the lower limit of the effect of increasing stock density on recruitment and was set at 0.75. The form of the second part of equation 2 is such as to splice, beyond equilibrium, for $Z > 1$, a declining exponential curve to the stock recruitment relation. The coefficient a_2 was set at 2.5.

(3) *Freshwater climatic effect* — The effect of climatic fluctuations was simulated with random normal deviates (RND), and after scaling to produce any desired range of extremes, augmented in absolute value by one and used as multipliers or divisors, depending on sign. The scaling coefficient, Q_1, was given values of 0.20715, 0.50000, and 0.61803, corresponding respectively to twofold, fourfold, and fivefold ranges of extremes, the first of which approximates the level of variability suggested by Adams River statistics. Algebraically, this step is

$$Z_2 = Z_1 ((\text{RND})\, Q_1 + 1), \quad \text{RND positive}$$

$$Z_2 = Z_1 \left(\frac{1}{(\text{RND})\, Q_1 + 1} \right), \quad \text{RND negative}, \qquad (3)$$

a procedure originally suggested by Ricker (1954) as appropriate for depicting environmental effects on salmon populations. This procedure does not generate a log-normal distribution of deviates, but a distribution somewhat similar to that form.

(4) *Depensation coefficients* — Simulated predation in the model varies in intensity according to the relation

$$Z_3 = Z_2 e^{a_3(v-1)}, \quad Z_2 < 1$$

$$Z_3 = Z_2, \quad Z_2 \geq 1, \qquad (4)$$

where Z_3 represents the smolt production, and where a_3, the total depensation coefficient, is given by $a_3 = a_{31}(Z_{2,t-1}) + a_{32}(Z_{2,t-2}) + a_{33}(Z_{2,t-3})$, the values a_{31}, a_{32}, and a_{33} expressing the effect of the fry production of the previous years ($Z_{2,t-1}$, $Z_{2,t-2}$, $Z_{2,t-3}$). The values of a_{31}, a_{32}, a_{33} were varied from 5,5,5 to 1,1,1, with all three being equal, and several series were run using declining coefficients such as 5,2,1, or 4,3,2. In all, nine combinations of coefficients were used. These depensation coefficients cause the basic dominance pattern, and their values reflect the effect of the abundance of fry on the survival of fry in subsequent years as mediated through the survival and growth of trout and other predators.

(5) *Smolt buffering coefficients* — In the relation given in equation 4 above, the parameter, v, is given by

$$v = s(Z_{3,t-1}) + Z_2, \qquad (5)$$

the coefficient, s, reflecting the degree of contribution made by smolts of a previous year to the total biomass of young salmon available to predators in a particular year. In different simulations, the value of s was varied from 0.0 to 0.15 at 0.05 intervals, this range being based on consideration of the observed biomass of smolts in relation to fry, and the length of time smolts are available as an alternative food for predators. More generally, the coefficient, s, could be taken to represent the total buffering provided by the dominant run, including dead eggs, 2nd year fry, and smolts.

(6) *Marine climatic effect* — Marine mortality is represented as a random factor in a similar fashion to that for freshwater climatic effects. The scaling factor (Q_3) used was 0.61803 corresponding to a fivefold ratio of extremes, a range approximating observed variations in rate of return of smolts as adults, i.e.,

$$Z_t = Z_3 ((\text{RND})\ Q_2 + 1), \quad \text{RND positive}$$

$$Z_t = Z_3 \left(\frac{1}{(\text{RND})\ Q_2 + 1} \right), \quad \text{RND negative,} \quad (6)$$

where Z_t is the production of recruits that survive to become adults at various years in the future.

The sensitivity simulations were 324 runs each of 50 simulated years, using all combinations of: nine sets of depensation coefficients; four values of the smolt-buffering coefficient; three values of the compensation coefficient; three values of the freshwater climate effect.

Each simulation started with initial conditions designed to imitate the natural situation in the year 1922 (simulated year 1) when there was observed a modest run of Adams River sockeye after several years of very low abundance following the effects of a logging dam and the 1913 blockage at Hell's Gate in the Fraser River canyon. The 6 years 1916–21 inclusive were each assigned abundances of .001 stock units (5000 fish), except for 1918, which was assigned an abundance of .01 stock units (50,000 fish). The estimated equilibrium stock size of 5 million fish is consistent with the estimate of $a_1 = 2.0$.

Results

The results of sensitivity simulations are summarized in Table 2. Because the model includes random factors, the form of fluctuation is in part determined by chance. Nevertheless, there are some strong trends evident in the results.

For depensation coefficients of 5-5-5 and 4-4-4, dominance forms on the 1st cycle year, in all instances within five cycles of 4 years. There is no development of subdominance.

For depensation coefficients of 3-3-3 (Table 2A), dominance forms on the 1st cycle year in those instances where the compensation coefficient is 2.0 or 1.5. With the higher value of 2.5, a "double dominance" on years 1 and 2 occurred with s = 0.10 at both lower values of Q_1. An almost perfect simulation of the historic record of the Adams occurred with s = 0.15 and Q_1 = .20715, a subdominant run changing to a dominant in year 42 of the simulation, corresponding to the calendar year 1963 (Fig. 1). These three simulations, marked in the Table as I, II, and III, were singled out for prediction studies (see below). In two other instances in the high range of climatic effects (Q_1 = 0.61803), patterns other than "single dominance" occurred and were notable for the development of dominance on year 4 as well as year 1. If the effect of dominance in nature is reflected in the machinery of the model, the development of a large run in the 4th cycle year is a less common alternative to development of a run in the 2nd cycle year.

With depensation coefficients 2-2-2 (Table 2B), dominance on the first cycle year only forms at the lowest compensation coefficient of 1.5. At the higher compensation coefficients the system quickly develops dominance on two or more years, more commonly D_1D_2 or D_1D_3. Only the simulations at high ranges of s and the intermediate value of the compensation coefficients show the form of fluctuation characteristic of the natural run. Two of these, marked IV and V, were chosen for prediction studies (see below).

For depensation coefficients 1-1-1 there are no characteristic fluctuations of the Adams River type. "Dominance" quickly develops in 3 of the 4 cycle years, or there is no pattern.

With depensation coefficients decreasing in magnitude, the situation is simulated in which the supposed effect of a dominant run, mediated through predators, decreases with each passing year (up to 3 years). These systems (Table 2, C and D give examples) produce (1) simple dominance on the 1st cycle year; (2) double dominance of years 1 and 3 or 1 and 4; or (3) unstable patterns with no regular dominance. None behave in a way that in suggestive of the natural pattern of the Adams.

In summary, it would seem that the types of fluctuations characteristic of the Adams run are related in the model to a relatively narrow range of coefficients. Because the model has random components, it is theoretically possible that a pattern like the natural series could appear with any set of parameters. However, it is apparent that those instances that produced appropriate patterns were those with parameters in the ranges as follows: (1) depensation coefficients (a_{21}, a_{22}, a_{23}) from 2-2-2 to 3-3-3; (2) compensation coefficients (a_1) from 2.0 to 2.5; (3) smolt buffering coefficients (s) from 0.10 to 0.15; (4) freshwater climatic effects in the lower range of variability (Q = 0.20715–0.50000).

The ranges indicated for the latter three variables coincide with estimates that may be made from data on the Adams River sockeye populations (Ward and Larkin 1964). The values for the depensation coefficients are essentially fitted by trial and error, made efficient by familiarity with the model system. The results of the simulations are gratifying in suggesting that the particular circumstances of the Adams run are necessary to the

TABLE 2. Patterns of population fluctuation in simulations of 50 years of Adams River sockeye populations with various combinations of parameters. D = dominant on cycle year of subscript; S = subdominant on cycle year of subscript. If pattern changes after sixth cycle, number over arrow indicates year of change. To be classed as dominant, a cycle year was repeatedly greater than 0.3 stock units; as subdominant, repeatedly greater than 0.01 stock units but less than 0.05 stock units. Where no pattern was sustained, the symbol N is used. Roman numerals mark special cases used in prediction simulations (see Table 3).

Compensation coefficient (a_1)	Scaling factor for climatic effects (Q)	Smolt buffering coefficient (s) 0.0	0.05	0.10	0.15
(A) Rates of fry depensation: a_{31}, a_{32}, a_{33} = 3-3-3					
				I	II
					42
2.5	0.20715	D_1	D_1	D_1D_2	$D_1S_2 \rightarrow D_1D_2$
				III	
	0.50000	D_1	D_1	D_1D_2	D_1
					35
	0.61803	D_1	D_1D_4	D_1	$D_1D_2D_4 \rightarrow D_2D_4$
2.0	0.20715	D_1	D_1	D_1	D_1
	0.50000	D_1	D_1	D_1	D_1
	0.61803	D_1	D_1	D_1	D_1
1.5	0.20715	D_1	D_1	D_1	D_1
	0.50000	D_1	D_1	D_1	D_1
	0.61803	D_1	D_1	D_1	D_1
(B) Rates of fry depensation: a_{31}, a_{32}, a_{33} = 2-2-2					
			30		
2.5	0.20715	$D_1D_2D_3$	$D_1S_2S_3 \rightarrow D_1D_3$	$D_1D_2D_3$	$D_1D_2D_3$
	0.50000	D_1D_2	D_1	D_1D_2	D_1D_2
	0.61803	D_1D_3	D_2D_4	D_1D_3	$D_1D_2D_4$
2.0	0.20715	$D_1D_2D_3$	D_1D_3	$D_1D_2D_3$	$D_1D_2D_3$
				IV	V
					26 42
	0.50000	D_1D_2	D_1	D_1D_2	$D_1 \rightarrow D_1S_2 \rightarrow D_1D_2$
	0.61803	D_1D_3	D_1D_4	D_1D_3	$S_1D_2D_4$
1.5	0.20715	D_1	D_1	D_1	D_1
	0.50000	D_1	D_1	D_1	D_1
	0.61803	D_1	D_1	D_1	D_1
(C) Rates of fry depensation: a_{31}, a_{32}, a_{33} = 4-3-2					
2.5	0.20715	D_1	D_1D_4	D_1	D_1D_4
	0.50000	D_1D_4	D_1	D_1D_4	D_1
	0.61803	D_1S_4	N	D_1	D_1D_4
2.0	0.20715	D_1	D_1	D_1	D_1
	0.50000	D_1	D_1	D_1	D_1
	0.61803	D_1	D_4	D_1	D_1D_4
1.5	0.20715	D_1	D_1	D_1	D_1
	0.50000	D_1	D_1	D_1	D_1
	0.61803	D_1	D_1	D_1	D_1

(*Continued*)

TABLE 2. Patterns of population fluctuation in simulations of 50 years of Adams River sockeye populations with various combinations of parameters. D = dominant on cycle year of subscript; S = subdominant on cycle year of subscript. If pattern changes after sixth cycle, number over arrow indicates year of change. To be classed as dominant, a cycle year was repeatedly greater than 0.3 stock units; as subdominant, repeatedly greater than 0.01 stock units but less than 0.05 stock units. Where no pattern was sustained, the symbol N is used. Roman numerals mark special cases used in prediction simulations (see Table 3). — (*Concluded*)

Compensation coefficient (a_1)	Scaling factor for climatic effects (Q)	Smolt buffering coefficient (s) 0.0	0.05	0.10	0.15
(D) Rates of fry depensation: a_{31}, a_{32}, a_{33} = 5-2-1					
2.5	0.20715	D_1D_3	D_1D_3	D_1D_3	D_1D_3
	0.50000	D_1D_3	D_1D_4	D_1D_3	D_1D_4
	0.61803	D_1D_3	N	D_1D_3	D_1D_4
2.0	0.20715	D_1D_3	D_1D_3	D_1D_3	D_1D_3
	0.50000	D_1D_3	D_1D_4	D_1D_3	D_1D_4
	0.61803	D_1D_3	32 $D_1D_4 \rightarrow D_4$	D_1D_3	36 $D_1D_4 \rightarrow D_4$
1.5	0.20715	D_1	D_1	D_1	48 $D_1 \rightarrow D_1D_4$
	0.50000	D_1D_4	D_1	D_1D_4	D_1
	0.61803	32 $D_1 \rightarrow D_1D_4$	36 $D_1D_4 \rightarrow D_4$	D_1	40 $D_1D_4 \rightarrow D_4$

nature of the population fluctuation, but are not so particular that some other pattern could not emerge, given a different sequence of environmental conditions.

The Element of Chance

The knowledge that a limited variety of alternative parameter values will produce patterns resembling that which occurs naturally leads to an interesting problem in further analysis. If the values of all of the parameters were known, one could run off several hundred replicate simulations, each with a different random number sequence, and thus estimate the probability that the Adams river sockeye would show a particular pattern of fluctuation in numbers. When the parameter values can only be approximated, there is no a priori reason for choosing one set as opposed to another, and there is the alternative of running one replicate for each of a large number of slightly different sets of parameter values. Table 3 summarizes data for a compromise between these extremes, 12 replicates for each of the combinations of variables marked as "cases" (I to V) in Table 2. The third row of the table indicates simulations that were "almost perfect" mimics of the natural pattern with subdominance switching to dominance between simulations years 30 to 50, corresponding to natural years 1951 to 1971. The second line of the table represents similar transitions in which the switch occurred before year 30 (1951).

Taking the array of results in aggregate as a "sample" suggests that the odds in the Adams situation in 1922 were 24 out of 60 of becoming dominant on a single cycle indefinitely; 19 of developing subdominance that becomes double dominance within 30 years; 10 of delaying subdominance until after the 30th year; and 7 of developing some other pattern. Of the 29 times subdominance became double dominance, the average timing corresponded to about the natural year 1951 or 1955, which is a fair approximation to the natural events. In the model, the timing of the pattern that develops largely depends on the accidents of random numbers, just as the natural situation is influenced by the "accidents" of climate.

Strikingly, in these special instances, whenever subdominance led to double dominance, it was a stable situation that did not lead to the development of a further change in pattern.

The Properties of Subdominance

When the simulations are examined in detail, it is clear that the development of subdominance

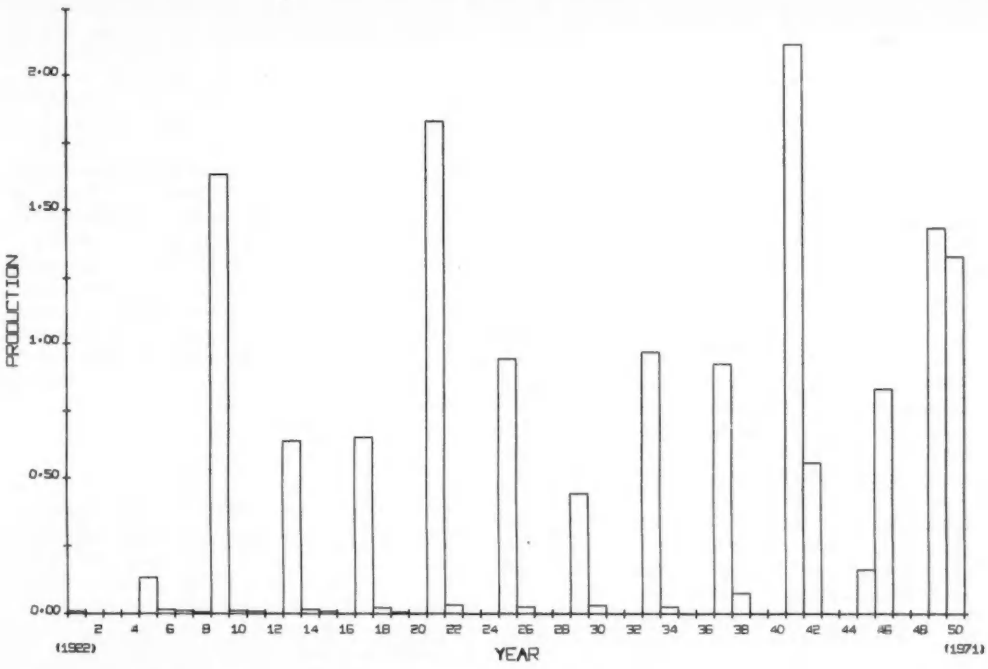

FIG. 1. A simulation of the years 1922–71 of the Adams River sockeye salmon population. Subdominance shifts to dominance in the 42nd year (1963). Because random deviates are used to simulate climatic effects, the simulation does not predict numbers for any year, but only the form of the population fluctuation. Production is in stock units of 5 million fish. See text for parameter values.

TABLE 3. Results of replication 12 times of the five "special" cases marked in Table 1, in which patterns occurred similar to the history of the natural Adams run.

Pattern	Case I	II	III	IV	V	Total
D_1	6	6	8	3	1	24
$D_1S_2 \xrightarrow{<30} D_1D_2$	2	4	3	4	6	19
$D_1S_2 \xrightarrow{30\text{–}50} D_1D_2$	4	2	1	–	3	10
Other	–	–	–	5	2	7
						60

depends on the combination of the depensation and smolt-buffering coefficients. As reported by Ward and Larkin (1964), subdominance in the model is not a stable situation once the subdominant run reaches the size that has occurred naturally. In the simulations, if the subdominant escapement reaches approximately .03–.05 stock units (150,000–250,000 fish), there is about an equal chance that it may become equal in size to the dominant run, or that it may shrivel to very small size. Depending on the chance elements, the transition into either state may take some time, it being only a question of when there is a sequence of appropriate "climatic effects."

This feature of subdominance is evident from looking at the deterministic structure of the model. The processes that are taking place for any generation, simplified, considering only the effect of the dominant cycle on the subdominant, and removing the age distribution and random factors, are:

$$Z_1 = we^{a_1(1-w)} \tag{2}$$

$$Z_2 = Z_1 e^{a_3(v-1)} \tag{4}$$

where

$$v = s(Z_{t-1} + Z_1). \tag{5}$$

Substituting equations 2 and 5 in 4, we have

$$Z_2 = we^{a_1(1-w)}e^{a_3(sZ_{t-1} + we^{a_1(1-w)}-1)}. \quad (6)$$

If the subdominant run is to increase in size from one generation to the next, then Z_2 must be greater than w. By setting Z_2 equal to w, and simplifying, it is readily deduced that the subdominant will increase when

$$a_1(1-w) + a_3(sZ_{t-1} + we^{a_1(1-w}-1) > 0. \quad (7)$$

The value of Z_{t-1}, the production of the dominant run, can be taken as 1.0 and a_3 may be taken as only the first depensation coefficient (say, 3). Then substituting 0.10 for s and 2.0 for a_1, and solving equation 7 by trials, the subdominant will increase when w, its spawning stock, exceeds approximately .03 stock units. When the subdominant is also large, a_3 will be approximately twice as great and, to increase, the run in the 3rd cycle year must exceed 0.10 stock units. In consequence, the double dominance situation is quite stable. When natural predators are provided with 2 years of high prey abundance, they can inflict such high mortality on the year-classes of the third and fourth cycles as to make their emergence as continuing large runs highly improbable.

Effects of the Fishery

It is a conspicuous feature of the foregoing that a simulated fishery has not been built into the model. Insofar as the major features of the form of the population fluctuation are concerned, this is of no great consequence. However, historically the fishery on Adams River sockeye may have had two effects that could have served to preserve a pattern of a dominant run and a subdominant run. By cropping the dominant to a level of approximately 2 million spawning fish, production has been much greater than would be the case at equilibrium. If production of fry is maximal in these circumstances, then depensatory effects on succeeding year-classes could conceivably be greater. If depensatory effects relate to egg deposition rather than fry production, then the fishery may have created circumstances more favorable to the development of subdominance.

Perhaps more pertinent is the second effect of the fishery — cropping the subdominant run at sufficiently high rates so that it is suppressed. Because the subdominant run is on odd years (1955, 1959, etc.), it is fished at the same time as every alternate run of pink salmon in the waters of south coastal British Columbia and adjacent United States.[1] In 1955 and 1959, the subdominant was harvested at rates of about 86 and 82% respectively, by contrast with rates of 78 and 71% for the dominant years 1954 and 1958.

In 1967, the subdominant run had 840,000 spawners after a fishery of approximately 73%, and thus showed prospect of developing into a large dominant run. It is thus expected that in 1971 the "subdominant" run could be large. (The current prediction of the International Pacific Salmon Fisheries Commission is 2.25 million, which is a relatively modest forecast.) If the foregoing model system is valid, the opportunity seems to have arrived for developing double dominance. Rates of harvesting of sockeye in odd-number years may be influenced by rates of harvesting of pink salmon, and vice versa, so that management decisions may be accordingly complicated.

Comment

In a nutshell, these model studies have suggested that, given the initial conditions of the early 1920's, there was about a 50:50 chance that the Adams run would either revert to its possible pre-1913 historic pattern of quadrenniel dominance (Ward and Larkin 1964), or assume some new pattern, most likely a pattern in which subdominance became double dominance after 20–40 years. Once double dominance is established, the system should have stability. Predator removals would have the effect of lowering depensation coefficients and permit the development of large runs on the off years as well.

These are properties of the model. Whether the natural system is as simple, or as rigid, is very doubtful, but until there is more information to put into a more complex model, it is the best sense that can be made of the situation (at least for me).

Technically, the structure of the present model leaves much to be desired. It has been argued (Holling 1968) that a "good" model has generality, holism, realism, and precision. The Adams River simulation has only a small measure of each of these qualities. It can be used to describe other sockeye salmon populations (for example, I have also used the model for simulating the Chilko River population and the results show fluctuations of the same form as the observed events); and with different parameter values can be used to simulate a wide variety of sockeye salmon fluctuations.

---

[1]The initial recovery of the Adams River run on the 1922 cycle, rather than the historic 1921 cycle, may well reflect the effect of the pink salmon fishery on the odd years.

The model is thus general only in the sense that it can be used to describe sockeye salmon biology. It lacks holism chiefly in not representing predators except by their effect on the prey, and the lack of any machinery of inheritance of age of return. Realism is an elusive property of models, except when they are viewed with hindsight. In its faithfulness to the representation of events in sockeye life history, the model has literal realism, but the representation of depensatory processes is essentially based on a deductive argument. The population fluctuations could only be caused if predators affect the prey in a certain way, and when they are made to act that way they produce the desired result. Indeed, a simple system that can be equally effective in imitating the form of the fluctuation is the equation

$$Z_t = w_t e^{a(1-w_t-\alpha w_{t-1}-\beta w_{t-2}-\lambda w_{t-3})}, \qquad (8)$$

which can be derived in an analogous fashion to the Ricker stock–recruit relation, making the assumption that the abundance of predators is related to the initial abundances of prey in any year and the 3 preceding years.

As for precision, the model system here described, because of its imitation of climatic factors by random deviates, produces a spectrum of answers. It is so imprecise as to be virtually untestable using historical data. Verification will require further field observation and experiment, hopefully of the kind that would lead to development of a better model system.

But for all of these shortcomings, the model demonstrates that relations of the kind one would postulate for predation have potential for generating the kind of fluctuation that the Adams River sockeye run has shown. An experimental program of predator removal is an obvious consideration for management, as is the possibility of regulation of the fishery for developing the subdominant run rather than suppressing it. Admittedly, the present pattern of 1 big year, 1 small, and 2 trivial, may maximize production from the Shuswap Lake system that the Adams River sockeye exploit. For example, Preston (1970) makes the argument that inequality of cycle years perhaps stabilizes the total salmon production at a maximum value; that equality of cycle years would enhance predator survivals; and that "the logical expectation is that the distribution [of abundance] will approximate to log normal, insofar as this is possible with only four subpopulations." The obvious inference is that, to be effective, efforts to increase the size of the subdominant and off-year runs should be coupled with predator control programs.

There remains the possibility that the dominance phenomenon has other causes, among which grazing effects on plankton, competition from or predation by kokanee, and mysterious genetic effects have been mooted (see Ward and Larkin 1964, for discussion). But in the absence of convincing evidence to support these alternative hypotheses, it seems appropriate to explore the possible benefits that the predation theory promises — large runs on 2 years, and perhaps large runs on 4 years by predator removals. Further research is perhaps warranted before taking the risk of jeopardizing such an important salmon production as that of the Adams River.

Dr W. E. Ricker has pointed out to me that the predation explanation for the Adams River fluctuation in abundance has other and more general implications for management of Fraser sockeye. Prior to 1913, all upriver stocks seem to have been dominant on the same year, implying the existence of an additional synchronizing depensatory mechanism in one or more of the lower river, the estuary, and the Strait of Georgia. Presumably, large numbers of seaward migrants from the Adams run would effectively saturate predators and enhance survival rates for other runs. Any numerical response of the predators would cause higher rates of mortality on seaward migrants of the succeeding 3 years. If this line of argument is correct, it may in part account for the relatively slow rate of recovery of some of the other upriver runs to their historic levels of abundance. They could only get the full benefit of lacustrine and estuarine depensation if they were synchronous on the same cycle. For both the particular case of the Adams River sockeye, and the more general questions of Fraser River sockeye management, research on predator–prey relations seems a profitable line for further investigation.

Acknowledgments

Mr L. Royal, former Director of the International Pacific Salmon Fisheries Commission, has encouraged these studies over the past several years, and has been helpful in providing advice and comment. The criticisms of Commission staff, particularly Mr J. Roos, have been valuable. F. C. Withler and W. E. Ricker read the manuscript and made important suggestions. Mrs D. Lauriente cheerfully looked after much of the tedium of computation.

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Size Selective Predation Among Juvenile Salmonid Fishes in a British Columbia Inlet

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PARKER, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Bd. Canada 28: 1503–1510.

Field observations suggest early sea mortality of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon fry is largely due to predation by juvenile coho (*O. kisutch*) salmon. A series of experiments demonstrates a strong bias toward the smaller individuals of the prey population. This results in an apparent growth rate 0.3–0.5% per day due to the biased mortality alone. With a high innate growth rate ($\bar{g} \sim 1.4\%$/day), the prey are shown to "outgrow" the predator ($\bar{g} \sim 0.7\%$/day), and hence become unavailable. Chums are shown to have an advantage over pinks through slightly earlier entry into the estuary and a larger initial size. The mechanism of selection used by the predator is not known from this study.

PARKER, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Bd. Canada 28: 1503–1510.

Des observations sur le terrain nous portent à croire que la principale cause de mortalité des saumoneaux roses (*Oncorhynchus gorbuscha*) et chum (*O. keta*) au début de leur séjour en mer est la capture par les saumons coho (*O. kisutch*) juvéniles. Des expériences ont démontré un biais prononcé en direction des proies de petite taille. Il en résulte un taux de croissance apparent de 0.3% à 0.5% causé par la seule mortalité faussée. Dotées d'un taux de croissance naturel élevé ($\bar{g} \sim 1.4\%$/jour), les proies semblent dépasser en grosseur les prédateurs ($\bar{g} \sim 0.7\%$/jour) et partant, cessent d'être disponibles. Les saumons chum ont sur les roses l'avantage de pénétrer plus tôt dans les estuaires et d'être au début plus gros que les roses. On ne peut déduire de cette étude le mécanisme de sélection des proies par les prédateurs.

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OF the 1961, 1962, and 1963 brood years of Bella Coola River pink salmon (*Oncorhynchus gorbuscha*), an estimated 56 million, 61 million, and 32 million fry, respectively, entered the estuary. During the first 40 days of marine life, losses, believed to be due primarily to predation by juvenile coho salmon (*O. kisutch*), were 77, 55, and 59%, respectively (Parker 1968). Predation at this intensity, if nonrandom, can exert a strong influence on the evolutionary development of the prey species and can persist for only a short time if the prey is to survive as a species.

Ivlev (1961) stressed that the type and degree of selectivity depends both on traits inherent in the predator and on qualities characteristic of the prey. Selectivity by a predator for a certain size of prey is typical of such an interdependence.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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Mortality can be biased in respect to size in several ways. In Ricker's (1969) view, the relation is usually such that larger members of a year-class are subjected to a higher mortality rate. Ivlev (1961) concluded that typically predatory fishes prefer to devour the largest possible prey. However, if the size frequency of the prey extends beyond the size of possible ingestion, this could lead to selectivity for either the middle-size or the smaller individuals present.

In this paper, mortality biased in respect to the size of the prey is considered.

Model

Notations used are as follows: l = length of the fish; t = time, and the unit is 1 day; $g = \mathrm{d}l/l\mathrm{d}t$, the relative instantaneous growth rate; $q = \mathrm{d}N/N\mathrm{d}t$, the instantaneous mortality rate; σ = the standard deviation of a distribution, σ^2 = variance, also abbreviated "var"; C = the coefficient of variation, given by $\sigma_x/\bar{x}$, x being any attribute. Also called the "relative standard deviation"; $c = \mathrm{d}C/C\mathrm{d}t$,

the relative instantaneous rate of change in C. A carat (^) is used over a value to indicate it is estimated from the data rather than a real or expected number. A (-) bar is used over a symbol to indicate a mean value.

The relative growth equation

$$l_t = l_0 e^{gt} \tag{1}$$

is employed and assumed appropriate. With no significant covariance between g and l, approximate variance of the distribution of l at t is given by

$$\text{var } l_t = (\bar{l}_t)^2 \,[\text{var } l_0(\bar{l}_0)^{-2} + t^2 \text{ var } g]; \tag{2}$$

that is, C^2 increases by the amount t^2 var g.

The significance of the increase in C^2 with growth was evaluated by trial calculations. Values for $l_0 = 35$ mm, $\sigma_l = 3.5$ mm, and for $g = 0.02$, $\sigma_g = 0.002$ were used. These are realistic values for fry when entering the estuary (LeBrasseur and Parker 1964). Results were:

t (*days*)	Length (*mm*)	C
0	35	0.100
10	43	0.102
20	52	0.109
30	64	0.117
40	79	0.128

In 20 days, under conditions of natural growth, the value of C is increased by about 10%. By restricting growth (suppressing ration) and by restricting the time period, the relative standard deviation of length can be assumed as constant in a population of fishes growing without size-biased mortality. Such a situation is depicted in Fig. 1 by the broken lines. Sample frequencies of lengths of the population at times 0 and t are plotted on a logarithmic scale. The distributions are expected to remain relatively the same, i.e., $C_0 \simeq C_1$. The range in size in arithmetic scale will increase. The instantaneous growth rate is represented by the slope of the line connecting the two means.

If a biased mortality is imposed, for example, of increased intensity for the smaller fish, then both g and C will be affected. This situation is depicted in Fig. 1 by the solid lines. In this instance, the estimate of the average growth rate, $\hat{\bar{g}}$, is larger than the true rate $\bar{g}$, and the coefficient of variation is decreased. Parallel arguments can be made to include the effects of biased mortality toward any particular subgroup classified by size.

Two linear regressions are proposed to describe these effects. The degree of bias per unit q is taken as constant.

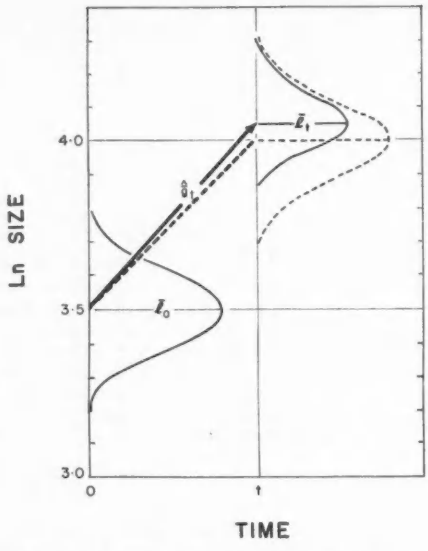

FIG. 1. Diagrammatic representation of the effect of mortality biased toward the smaller individuals on the estimated ($\bar{g}$) average instantaneous growth rate.

$$\hat{\bar{g}} = a_1 + b_1 q \tag{3}$$

$$c = a_2 + b_2 q. \tag{4}$$

Parameters of equations 3 and 4 are estimated from several sets of g, C, and q where q is deliberately varied.

From these regressions the following inferences can be made:

(1) Intercept a_1 estimates $\bar{g}$ in the absence of mortality. It is the best unbiased estimate of the true average relative growth rate.

(2) Where intercept a_2 is positive, growth has been biased in favor of the larger fish.

(3) Where a_2 is 0, growth has been unbiased.

(4) Where a_2 is negative, growth has been biased in favor of the smaller fish.

(5) Where slope b_1 is positive, mortality has been biased toward the smaller fish.

(6) Where b_1 is 0, there has been either (*a*) no bias (confirm by 9 below), (*b*) bias for the middle sizes (confirm by 8 below), or (*c*) a balanced bias for both large and small (confirm by 10 below).

(7) Where b_1 is negative, mortality has been biased toward the larger fish.

(8) Where b_2 is positive, mortality has been biased toward the middle sizes.

(9) Where $b_2 = 0$, mortality has been unbiased in respect to size.

(10) Where b_2 is negative, mortality has been biased for either (*a*) the larger fish (confirm by 7 above), or (*b*) the smaller fish (confirm by 5 above), or (*c*) a balanced bias for the tails of the distribution (confirm by 6 above).

The effect of var g is to bias a_2 by increasing its value. Although this effect cannot be distinguished from that of biased mortality, the error introduced is relatively small and not likely to affect the interpretation of results.

Materials and Methods

Juvenile pink, chum, and coho salmon were obtained in Burke Channel with a small seine. These were transported to an anchored laboratory barge and held in floating cages until the next day. Twelve prey populations were established, each containing about 500 fish In establishing the population, the length of each fish was recorded on millimeter paper while under anaesthesia (2-phenoxyethanol). After a recovery period of about 4 hr, three coho were similarly treated and introduced as predators into each of eight aquaria containing prey populations. The remaining four prey populations were held without predators. One of the predator–prey populations was lost early in the experiment. The remaining 11 were held until about 50% of the prey had been killed in some of the groups. At this time the set of experiments was terminated, and the survivors anaesthetized and measured.

Each aquarium held about 200 liters of sea water, which was replenished by a constant supply, flowing at about 4 liters/min. Food was restricted to that available in the sea water, which was pumped from a depth of about 2 m. Some fish died during the experiment but were not consumed. These were removed daily and are included in the mortality and growth calculations but not in calculations of rates of consumption for the predators.

Results

Length-frequency histograms of the prey populations (without respect to species) at initiation and termination of the experiments are shown in Fig. 2. It is seen that the size distributions of prey populations were altered when predators were present (aquariums 5–11). Population statistics and the resulting values of q, g, and c are given in Table 1. In Fig. 3, g is plotted as a function of q, and a linear regression line, calculated by the method of least squares for all observations, is shown. Differences between the pink and chum relations are probably not significant and are ignored. The intercept $a_1 = 0.0019$, $\sigma_{a_1} = 0.00023$ (12%), and the slope $b_1 = 0.14$, $\sigma_{b_1} = 0.016$ (11%). In Fig. 4, c is plotted as a function of q, and a linear regression line, calculated from all data by least squares, is shown. Differences between the pink and chum relations again do not appear to be significant. The intercept $a_2 = -0.0005$, $\sigma_{a_2} = 0.00127$. The slope $b_2 = -0.79$, $\sigma_{b_2} = 0.078$.

From these results, it is inferred that the true growth rate under the imposed environmental conditions was $\bar{g} = a_1$. The value of a_2 is close to and, by inspection, not significantly different from 0. Accordingly (inference 3) growth rate was probably unbiased with respect to size. The slope b_1 is positive. Therefore (inference 5) mortality was biased toward the smaller individuals. This is confirmed as among the three possible interpretations of a negative slope b_2 (inference 10). The amount of bias in $\hat{g}$ is estimated from its effect in units of $\bar{g}$ per unit of q, i.e., b_1, which is, in these data, 0.14 units of $\bar{g}$ per unit of q. Initial and terminal length measurements of the predators are given in Table 2. Growth rates of individuals varied from 0.2 to 1.2%/day. Among the seven predator populations, the average instantaneous growth rates were more uniform, varying only between $\bar{g} = 0.00490$ and $\bar{g} = 0.00774$. The average of all populations is about 0.7%/day. Average rates of consumption of prey among the seven predator populations are included in Table 2. The actual consumption of prey by each predator is not known. Among experiments, the average rate of consumption of prey varied more than fourfold, reflecting (in part) differences in size composition of the prey populations available to a particular set of predators (see Fig. 2). The number of prey making a daily ration tended to be greater when smaller prey were available, and vice versa.

Discussion

Ricker (1969) demonstrated the several different growth rates that may be derived from "back-calculated size-at-time data.[1] Such estimates generally show the following relations within a given year-class:

$$\begin{array}{cccc} \bar{l}_{1.1} & \bar{l}_{2.2} & \bar{l}_{3.3} & \bar{l}_{4.4} \\ \uparrow & \uparrow & \uparrow & \\ \bar{l}_{1.2} & \bar{l}_{2.3} & \bar{l}_{3.4} & \\ \uparrow & \uparrow & & \\ \bar{l}_{1.3} & \bar{l}_{2.4} & & \\ \uparrow & & & \\ \bar{l}_{1.4} & & & \end{array}$$

[1]A procedure where the position of a mark on a bony part is measured, and by means of a body: part relative size relation, the length of the fish at the time the mark was made is estimated.

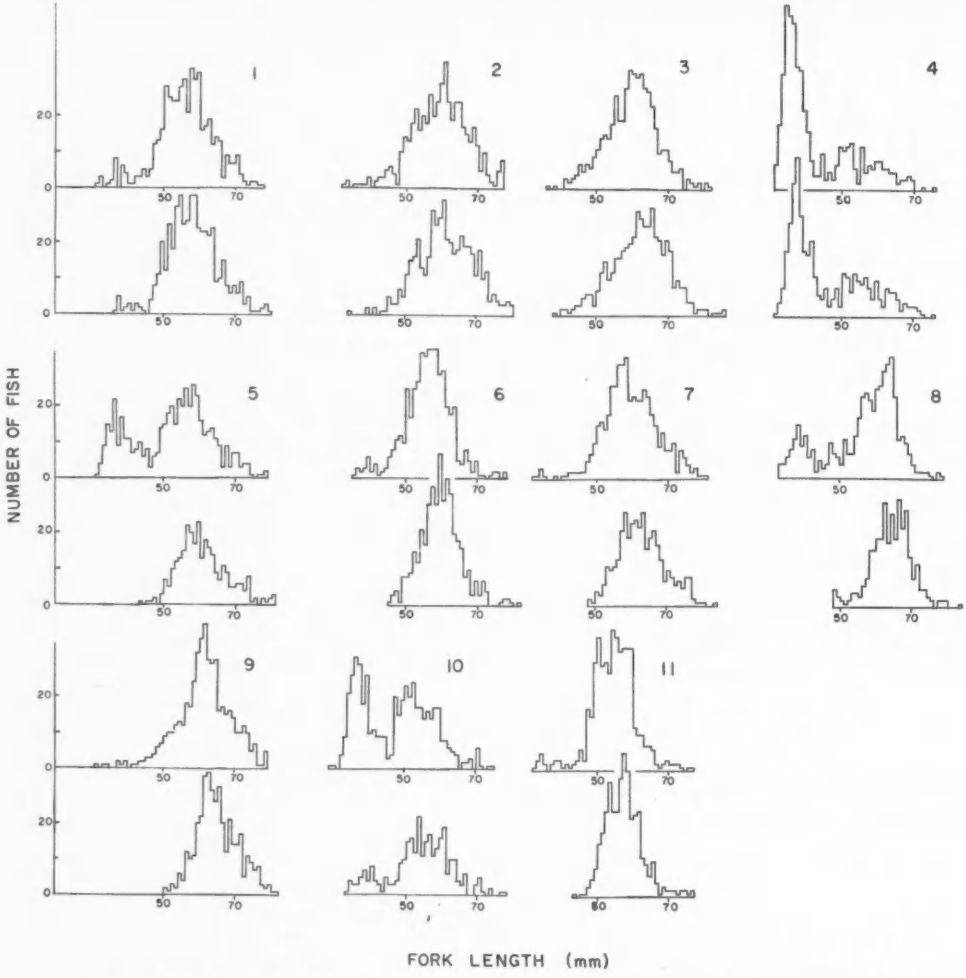

FIG. 2. Initial (*top*) and terminal (*bottom*) length-frequency histograms of each prey population.

The first numeral in the subscript refers to the estimate of average length at age = 1, 2, etc. The second numeral refers to the age of the specimens from which the estimate was made. The arrows denote the direction of the larger estimate, and the schematic portrays positive "Lee's Phenomenon," which refers to an apparent negative correlation between growth rate and survival (see Ricker 1969).

Among the possible growth rates, two sets were considered.

(1) For the 4th growth year $\ln(\bar{l}_{4.4}/\bar{l}_{3.4})$

3rd growth year $\ln(\bar{l}_{3.3}/\bar{l}_{2.3})$

2nd growth year $\ln(\bar{l}_{2.2}/\bar{l}_{1.2})$.

These were termed "true instantaneous growth rates," even though, as noted by Ricker (1969 p. 493), the back-calculated values represent only that portion of the year-class that survived the preceding year.

TABLE 1. Survival and growth statistics of prey populations. N_1, N_2 denote initial and terminal population size; q the instantaneous mortality rate; $\bar{l}_1$ and $\bar{l}_2$ the initial and terminal average length of fish in the populations; g the instantaneous growth rate; C_1, C_2 the initial and terminal coefficients of variability; c the instantaneous rate of change in C. Instantaneous rates are on a per day basis.

Aquarium no.	Duration (*days*)	N_1	N_2	q	$\bar{l}_1$ (*mm*)	$\bar{l}_2$ (*mm*)	$\bar{g}$	C_1	C_2	c
					Pinks					
1	18	401	401	0.00000	54.8	56.7	0.00189	0.1288	0.1148	−0.00642
2	17	253	239	0.00334	55.6	58.0	0.00241	0.1309	0.1222	−0.00403
3	15	100	96	0.00272	56.9	58.1	0.00150	0.1094	0.1086	−0.00048
4	17	500	420	0.01025	43.2	45.9	0.00352	0.2371	0.2289	−0.00207
5	13	402	186	0.05928	50.2	58.9	0.01224	0.2006	0.0931	−0.05904
6	16	399	336	0.01074	55.1	58.6	0.00389	0.1134	0.0811	−0.02092
7	17	251	151	0.02989	56.4	60.8	0.00443	0.1213	0.0876	−0.01914
8	16	248	108	0.05195	50.7	61.9	0.01242	0.1981	0.0809	−0.05594
9	18	100	25	0.07701	53.8	63.2	0.00894	0.1329	0.0564	−0.04753
10	17	503	296	0.03119	48.1	54.5	0.00734	0.2024	0.1573	−0.01484
11	17	502	391	0.01469	55.0	58.0	0.00314	0.1204	0.0915	−0.01615
					Chums					
1	18	100	100	0.00000	63.9	65.2	0.00115	0.1120	0.1050	−0.00357
2	17	250	239	0.00264	63.4	65.6	0.00199	0.1091	0.1044	−0.00255
3	15	401	396	0.00083	61.1	63.6	0.00268	0.1194	0.1260	0.00358
4	17	0								
5	13	100	97	0.00234	63.6	66.2	0.00310	0.1025	0.1042	0.00124
6	16	100	99	0.00062	61.1	63.7	0.00257	0.1122	0.1160	0.00204
7	17	249	223	0.00648	63.7	65.4	0.00160	0.1080	0.1004	−0.00424
8	16	248	232	0.00416	63.3	66.5	0.00304	0.0941	0.0936	−0.00034
9	18	398	368	0.00435	63.7	65.7	0.00168	0.1011	0.0911	−0.00581
10	17	0								
11	17	0								

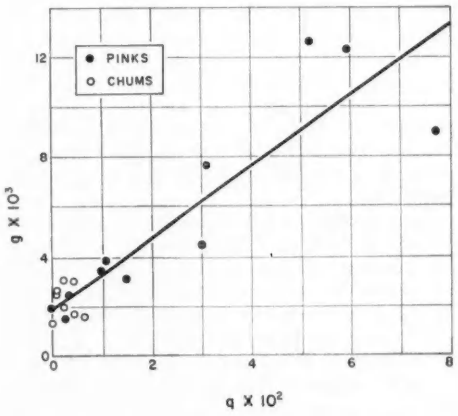

FIG. 3. Regression of instantaneous growth rate (g) on the instantaneous mortality rate (q).

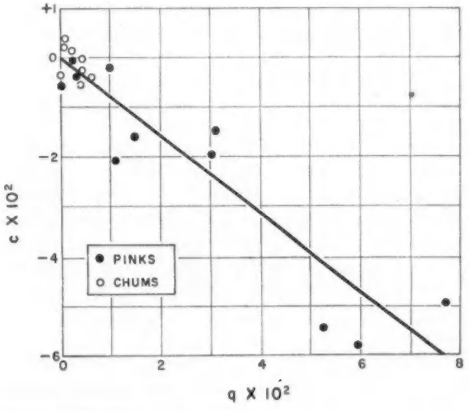

FIG. 4. Regression of instantaneous rate of change of coefficient of variance (c) on the instantaneous mortality rate (q).

TABLE 2. Initial and terminal lengths of predators, instantaneous growth rates and prey consumed.

Aquarium no.	t (days)	Fork length (mm) l_1	Fork length (mm) l_2	$\hat{g}$/day Individual	$\hat{g}$/day Avg	Total no. prey eaten	Prey per predator/day
5	13	105	116	0.00769	0.00708	207	5.31
		123	133	0.00600			
		136	150	0.00754			
6	16	111	115	0.00225	0.00490	60	1.25
		119	131	0.00600			
		120	133	0.00644			
7	17	101	123	0.01159	0.00741	110	2.16
		126	137	0.00494			
		127	140	0.00571			
8	16	90	108	0.01144	0.00738	146	3.00
		120	127	0.00356			
		132	148	0.00713			
9	18	113	128	0.00694	0.00720	90	1.67
		115	134	0.00850			
		128	143	0.00617			
10	17	119	124	0.00241	0.00680	188	3.69
		119	135	0.00741			
		122	146	0.01059			
11	17	112	126	0.00694	0.00774	100	1.96
		124	142	0.00794			
		125	144	0.00835			

(2) For the 4th growth year $ln\ (\bar{l}_{4.4}/\bar{l}_{3.3})$
3rd growth year $ln\ (\bar{l}_{3.3}/\bar{l}_{2.2})$
2nd growth year $ln\ (\bar{l}_{2.2}/\bar{l}_{1.1})$.

These were termed by Ricker "X"-type instantaneous growth rates, estimated by comparing the sizes of the surviving fish sampled at successive ages.

The apparent growth rates ($\hat{g}$) of this paper, then, correspond to Ricker's Type X. What I have termed the "true instantaneous growth rates" are what would be expected from the population under prevailing environmental opportunities, in the absence of biased mortality. Assuming unbiased growth, they are identical with Ricker's "True Growth Rate."

Jones (1958) treated the problem of size-biased mortality as a basis of Lee's Phenomenon. His model stipulated two unique conditions: (*a*) a normal distribution of size within the population, and (*b*) a positive linear relation between the instantaneous mortality rate and size, i.e.,

$$q_i = \alpha + \beta l_i.$$

Given these conditions, Jones (1958) demonstrated a decrease in the mean size due to biased mortality alone: $D = \beta\sigma_l^2$. Furthermore, the distribution remains normal, and the σ remains the same. β can also be a negative number, reflecting a decrease in mortality rate with increase in size. This condition would, as in the experiments reported in this paper, lead to an increase in mean size from biased mortality alone.

In equation 3, a_1 is the average growth rate under conditions of unbiased mortality, and $\hat{g}$ is the observed relative growth rate for each population. Given the conditions specified for the Jones relation,

$$\beta\sigma_l^2 = l_0 - l_0^{(\hat{g}-a_1)}. \qquad (5)$$

Experimental values of β for each prey population are calculated and given in Table 3. The time period used in these calculations is 1 day. Some obvious features are:

(1) the relatively high β values (>0.100) were obtained only in aquaria containing predators;

(2) β values <0.100 are obviously part of the error propagated in the system. For example, a value of -0.0009 was obtained for the chum population in aquarium 1, where no mortality occurred. This is traceable to the fact that, in that instance, the growth rate was less than 0.0019;

(3) the β values are quite dissimilar even in supposedly similar situations among aquaria, i.e., aquaria 5 and 6, 7 and 8, 10 and 11, in respect to pinks.

TABLE 3. Calculation of β and r values as indices of selectivity. See text for explanation of symbols.

Aquarium no.	$\bar{l}_0$ (mm)	$\hat{g}-a_1$ (10^{-3})	D (mm)	σ_0^2	$-\beta$ ($\times 10^{-3}$)	r
			Pinks			
1	54.8	0	0	49.8	0	0
2	55.6	0.5	0.028	53.1	0.5	0.0052
3	56.8	-0.4	-0.023	38.7	-0.6	-0.0050
4	43.2	1.6	0.069	104.9	0.7	0.0091
5	50.2	10.3	0.517	101.6	5.1	0.0697
6	55.1	2.0	0.110	39.0	2.8	0.0238
7	56.4	2.5	0.141	46.8	3.0	0.0278
8	50.7	10.5	0.532	100.9	5.3	0.0712
9	53.8	7.0	0.377	51.2	7.4	0.0364
10	48.1	5.4	0.260	94.8	2.7	0.0361
11	55.0	1.2	0.066	43.9	1.5	0.0134
			Chums			
1	63.9	-0.7	-0.045	51.2	-0.9	-0.0085
2	63.4	0.1	0.006	47.9	0	0
3	61.1	0.8	0.049	53.3	0.9	0.0091
5	63.6	1.2	0.076	42.5	1.8	0.0157
6	61.1	0.7	0.043	47.1	0.9	0.0084
7	63.7	-0.3	-0.019	47.3	-0.4	-0.0037
8	63.3	1.1	0.070	35.6	2.0	0.0158
9	63.7	-0.2	-0.013	41.5	-0.3	-0.0027

Ricker (1969) verified and used Jones (1958) relations as a basis for his "index of intensity of selection" (r). Using the present notation:

$$r = 1.349\beta\sigma_0. \quad (6)$$

The selectivity index (r) is equivalent to the difference in average instantaneous mortality rates of the smaller half and the larger half of the population. The selectivity index is independent of mean size and thus comparable among populations having dissimilar mean sizes.

Values of r were calculated for each prey population assuming the conditions specified for the Jones relation. Results are presented in the last column of Table 3. One is immediately struck by the heterogeneity of the results. Although Ricker (1969) assures us that the conditions specified for the Jones relation need not be rigorously obeyed, some distributions in the present experimental populations are not even approximately normal, i.e., 5, 8, and 10. Furthermore, there is no knowledge of the functional relation between q and size. It is suspected, then, that both of Jones' (1958) basic premises are sufficiently violated to produce the observed heterogeneity of r. There is also the possibility that the degree of selectivity was highly variable among the experiments.

Ivlev (1961) concluded, from a series of experiments using pike and perch as predators, that selection was generally for the largest prey within the size range that could be ingested. The present series of experiments are at fault for not including determinations of the maximum size of prey acceptable to each predator. Ivlev's findings may well explain the observed overall selection for the smaller fish if a maximum available size of, say, approximately 50-mm prey is postulated. The same principle could, of course, explain observed selectivity for any other subgroup of a population classified by size.

The mechanism of selectivity cannot be discovered from the present data. There can be little doubt, however, that the smaller prey suffered a higher mortality rate in the predator–prey situations simulated in the experiments. The application of this generalization to the interacting species in the natural environment reveals a fascinating example of species interaction.

In the Bella Coola River, pink alevins mature into fry within the spawning gravels, from which they ascend and immediately migrate seaward. The period of emergence (hence migration) is fairly prolonged, generally from early to late April, with maximum numbers appearing about the 20th. In this stage no significant feeding occurs, the energy source being embryonic stores. They are quite uniform in size, from 33 to 37 mm length, with a mean size of about 35 mm.

Chums also spawn in the Bella Coola system. Their time of out-migration slightly precedes but overlaps that of the pinks, and their average initial size is larger, about 38 mm. In the estuary, chums and pinks are usually found together in the same aggregations.

The Bella Coola River is also a spawning ground and nursery area of a considerable population of coho. This species spends 1 or more years after emergence in the stream, so that parr in a size range 100 ± 20% mm are present along the migration route of the pink and chum fry. Very little is known about the predator–prey interactions during this period. Our own unpublished observations of coho, obtained in the lower reaches of the Bella Coola during this period, indicate that the predominant food supply utilized by coho is fry. At this stage the more-or-less fixed predator populations must have a depensatory effect on each day's fry migration. Only when fry numbers exceed the predator demand will significant numbers appear in the sea.

These "spurts" of fry accumulate in the estuary and gradually disperse, but without active migration. Feeding begins in the estuary and growth is rapid. These conditions lead to frequency distributions in catches that are not normal but are composed of "age-groups," age here being reckoned in days. Examples of these distributions were shown by LeBrasseur and Parker (1964).

Toward the end of the pink fry migration the coho parr become smolts and enter the estuary. Here the utilized (but not obligate) prey is still pink and chum fry. In effect, if not by design, the prey has ceased coming to the predator so the predator has come to the prey.

It has been shown that there is a strong selectivity on the part of the predator for the smaller individuals of prey. Being "smaller" results from (1) a later entry into the estuary, i.e., being younger, (2) from growing slower, or (3) from being a pink rather than a chum.

From the experiments reported here it was seen that, under ad libitum feeding conditions, the juvenile coho grew at an average of about 0.7% in length per day. LeBrasseur and Parker (1964) reported pink fry in Burke Channel grow at about 1.8% per day. The fact that an appreciable amount of this growth rate (between 0.3 and 0.5) is probably due to predator selectivity does not alter the results: members of the prey population simply outgrow the predators and hence become unavailable. This is a very effective "turning off" mechanism.

The chums, in this situation, appear to have evolved a strategy to enhance their survival in a dangerous situation. The pink populations are usually numerically superior, sometimes by several orders of magnitude. As juveniles, chums are almost indistinguishable from the pinks in appearance. They are larger, as unfed fry, and enter the estuary during the earlier part of the pink migration. Although mortality is undoubtedly high in the downstream migration, by the time the predator population reaches the estuary, chums are among the larger members of the prey population. The chums are, then, buffered against the predator population by the smaller and later-arriving pinks.

In Burke Channel, juvenile coho may serve man a useful role in preserving and even reinforcing those characteristics that make pink salmon a valuable commercial species. Their selective predation must maintain and even strengthen the high innate capacity for growth. Selection of the smaller members must also enhance disease and parasite resistance, for not to grow means increased probability of early death. On the other hand, the effects of the nonobligate predator on the prey are depensatory. It is possible that if the prey population is brought to a low level by adverse conditions, it will be held there or driven to extinction unless predator pressure is relieved.

Acknowledgments

Field and experimental observations were made in 1967. Messrs R. C. Wilson and T. Cleugh were responsible for securing and establishing the test populations and their size-frequency data. The analytical model resulted from discussions with Dr J. Calaprice and Mr K. R. Allen. A précis was presented to the Annual Meeting of the American Fisheries Society at Toronto, September 15, 1967, and, again, the author benefited from the ensuing discussions with several colleagues. Dr J. Walker critically reviewed the final manuscript. To these people, named and unnamed, I express my gratitude.

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Aspects of the Characterization, Identification, and Ecology of the Bacterial Flora Associated with the Surface of Stream-Incubating Pacific Salmon (*Oncorhynchus*) Eggs

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Stream-incubating eggs of chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon usually appeared to have a characteristic bacterial flora associated with the radiate membrane or "capsule," *Cytophaga* spp. predominating over pseudomonads and other species. In comparison, populations on simulated egg surfaces (polyethylene spheres) consisted mostly of *Pseudomonas* spp. and *Chromobacterium lividum*, suggesting that the surface of the incubating egg is bacteriologically selective. The bacterial flora of dead eggs consisted mostly of *Pseudomonas* spp., whereas the ambient stream waters contained members of *Acinetobacter*, *Aeromonas*, *Enterobacter*, and two actinomycetes in addition to members of the genera found on eggs and "simulated eggs."

Some characteristics of the bacteria found associated with the surface of the embryonated egg are examined in relation to egg survival. The embryonated egg is regarded as part of a dynamic ecosystem, coined the "oosphere," and it is suggested that egg mortality probably depends more upon the results of complex interactions between the egg, its microflora, and its ambient waters than upon the presence of an obligate pathogen.

BELL, G. R., G. E. HOSKINS, AND W. HODGKISS. 1971. Aspects of the characterization, identification, and ecology of the bacterial flora associated with the surface of stream-incubating Pacific salmon (*Oncorhynchus*) eggs. J. Fish. Res. Bd. Canada 28: 1511–1525.

Les oeufs de saumon chum (*Oncorhynchus keta*) et roses (*O. gorbuscha*) en voie d'incubation en rivière possèdent généralement une flore bactérienne caractéristique associée à la membrane radiée ou "capsule," et où *Cytophaga* spp. l'emportent sur les pseudomonades et autres espèces. Par contre, la flore bactérienne qui se fixe sur des surfaces artificielles (sphères de polyéthylène) est constituée surtout de *Pseudomonas* spp. et *Chromobacterium lividum*, signe de la sélectivité bactérienne de la surface de l'oeuf en voie de développement. La flore bactérienne d'oeufs morts est constituée en grande partie de *Pseudomonas* spp., alors que les eaux ambiantes contiennent des représentants d'*Acinetobacter*, *Aeromonas*, *Enterobacter* et deux actinomycètes, en plus des genres trouvés sur les oeufs réels et "simulés."

Les auteurs examinent quelques caractéristiques des bactéries de la surface de l'oeuf au stade de l'embryon et leur influence sur la survivance de l'oeuf. Ils considèrent l'oeuf à ce stade comme faisant partie d'un écosystème dynamique pour lequel ils inventent le terme "oosphère." Ils croient que la mortalité de l'oeuf dépend probablement plus d'interactions complexes de l'oeuf, sa microflore et les eaux ambiantes que d'un organisme obligatoirement pathogène.

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NUMEROUS observations by fisheries biologists (Ricker 1962; McNeil et al. 1964; McNeil 1966) have led to the speculation that microorganisms, particularly bacteria, might be at least partly responsible for some mortalities of salmon eggs incubating either in stream gravel or in hatchery trays. This speculation was strengthened by the observations of Oppenheimer (1955) and Shelbourne (1965), which suggested that bacteria and other microorganisms can cause mortalities of marine fish eggs. It appeared to us that study of the microbial ecology of the surface of the "normal," healthy, incubating egg (assumed to have a "germ-free" embryo) was a prerequisite to assessing the role of microorganisms as possible agents of natural mortality. That is, it seemed essential to define or characterize, if possible, the "normal" before investigating the "abnormal" or pathological state of both the egg and what one might call the "oosphere" (cf. "rhizosphere"). We therefore attempted initially to isolate, describe, and identify the bacterial species found associated with the surfaces of living, dead, and "simulated" eggs as well as to study, in another project (Bell et al. 1969), the structure and function of the egg "capsule" or radiate membrane. Accounts of our preliminary results concerning the bacterial flora on salmon eggs have been given (Bell 1966; Bell and Hoskins 1967) and subsequent, more detailed results are reported here.

Materials and Methods

EGGS AND HOLDERS

Fertilized eggs were obtained by routine procedures from pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon and were thoroughly washed and hardened in the stream before being placed in holders for incubation.

To determine whether or not eggs presented a unique, biologically active surface or acted only as an inert support for microorganisms, we also incubated sterilized polyethylene spheres[1] (0.6 cm in diameter) under conditions similar to those for the eggs. The etched glass spheres previously employed (Bell 1966) could not be used because they often broke the dilution blank when it was vigorously shaken. These "simulated" eggs were then treated in the same manner as the real eggs. The ideal simulated egg surface would have been the isolated radiate membrane (invalidly, but commonly, called the "capsule," "chorion", or "shell"; Hurley and Fisher 1966) itself but it is impossible to obtain it intact. We had little success in incubating pieces of radiate membrane as a practical compromise because they were usually washed away.

Eggs with and without gravel were placed in holders of various designs so that they could be removed from the stream with minimum contamination by microorganisms associated with intergravel silt and detritus. The permeable plastic tubes containing mixtures of eggs and gravel used in earlier work (Bell 1966) were used to isolate cultures 1–48 but were subsequently replaced by plastic clamps, which substantially reduced many sources of bacterial contamination. The clamp (Fig. 1A) consisted of two plastic strips with rounded shallow wells top and bottom to hold the eggs firmly but with maximum exposure of their surface area. Holes were drilled through the wells to aid further in the irrigation of the eggs. There should thus have been minimum contamination of the sample by bacteria associated with the methacrylate plastic. Tension on the clamp was adjusted with nylon bolts, and plastic washers were used to prevent excessive pressure on the eggs. The clamps were mounted on stainless steel bolts embedded in a concrete block (Fig. 1B) and the unit was protected by a plastic cover (Fig. 1C) with a $1/2'' \times 3''$ slit at the upstream and downstream ends to allow water flow. A hinged aluminum lid permitted easy access to the sample.

There were few mortalities among eggs incubated in the plastic holders, and although there were, in contrast to the redds, no associated insects, a causal relation (Astafyeva 1964) should not be assumed. Some silt accumulated at the base of the concrete block but, the holders themselves usually remained quite clean.

INCUBATION SITES

Controlled flow spawning channels (free of salmonids) in the Big Qualicum River (Clay and Fahlman 1962) and Robertson Creek, both on Vancouver Island, were used for egg incubation, the former for 2 years and the latter for 1 year. Both streams are fed by oligotrophic lakes and the water was usually very clear, although heavy run-offs made the water slightly turbid on occasions during the egg incubation. The upstream ends of the channels were used because there was minimum siltation and no human disturbances. Under these conditions, it seems reasonable to assume that stream water and channel water were identical.

SAMPLING AND TRANSPORT

Eggs and polyethylene spheres were removed from the clamps using aseptic techniques and each was placed in a sterile, ice-cold dilution blank. (Any loosely adhering silt or detritus was washed off before the eggs were removed by placing the clamp in the natural water flow for a few minutes.) Dilution blanks were prepared from filtered heat-sterilized water taken from the stream in which the eggs were incubating. The time between sampling and plating was usually 3–4 hr. Samples were taken for bacteriological examination, usually at 1–2-week intervals, over the entire incubation period.

EXAMINATION OF BACTERIA

Eggs were exposed to osmic acid vapour for 3–5 min and were then stained in 1% methylene blue for

[1]Ace Plastic Co., Jamaica, New York.

5 min. The radiate membrane was removed and portions were mounted in water under a cover slip for microscopic examination.

A scanning electron microscope was used to obtain photomicrographs (Fig. 2) of bacteria on the surface of eggs. (Details of the method used will be published elsewhere.) Although the instrument offers great possibilities for studying in situ mechanisms of attachment of bacteria to surfaces and for examining natural topographic features (Gray 1967), much care must be taken to account for possible artifacts. We therefore will not speculate on the origin and function of the fibrous material shown in Fig. 2A and B until further work is done, particularly on stream-incubating chum and pink eggs.

In enumeration of bacteria, tubes containing iced samples of individual eggs and of plastic spheres were vigorously agitated for 2 min using a mechanical "tube buzzer."[2] Although this procedure removed most bacteria, some remained firmly fixed to the egg surface even with the addition of 1:1000 Tween 80 to the wash water. Sonic vibration at 20 kHz for even brief periods appeared to kill more bacteria than it removed from the egg surface, and homogenization of the egg in physiological saline released substantial quantities of interfering oils. Both swab (Douglas 1968) and direct count techniques were considered inappropriate because growth was very unevenly distributed over the egg surface (Fig. 3). In addition, this small round surface was inherently difficult to sample by these methods.

Plate counts, which had the added advantage of providing colonies for study, were then carried out using tryptone glucose extract agar (TGE) according to the methods of the American Public Health Association (1965) but incubation was at 25 C. Even though extension of the incubation period to 10 days resulted in increased counts (as also noted by Robohm and Graikoski (1966)), we did all counts at 72 hr using a "Bactronic Colony Counter Model C 110."[3] In retrospect, it would probably have been more suitable to use the drop plating method of Miles and Misra (1938) for the counts and isolations to avoid exposing sensitive cells to ca. 44 C for even brief periods.

Selection of Colonies

Macroscopically different colonial types that occurred most frequently on plates inoculated from live, dead, and "simulated" eggs and with stream water were selected at various times during the egg incubation period. They were then maintained for detailed study after they had been checked for purity. This method of selection should give a reasonably unbiased representation of the population associated with eggs at all stages of development (see Shewan et al. 1960 for another method).

[2]Hallikainen Instruments, Berkeley, California.

[3]New Brunswick Scientific Co. Inc., New Brunswick, New Jersey.

Characterization and Identification of Isolates

Unless otherwise stated, tests for identification and characterization were done according to the Difco Manual, 9th edition,[4] its Supplementary Literature issued in 1962, and the Manual of Microbiological Methods (Anon. 1957). Unless otherwise stated, all media and their components were supplied by Difco Laboratories. All chemicals were reagent grade.

The morphological characteristics studied were as follows.

Shape and size were determined from Gram stains of 24-hr broth cultures.

Motility was most readily and reliably detected by microscopic examination of the edge of 12–24 hr growth on agar containing low nutrient concentrations (e.g., 0.25% rather than 0.5% tryptone). A no. 1½ cover slip was placed over the growth on a thin block of medium and the cells carefully examined immediately under a 40× or 100× objective. Failure to realize the crucial importance of adhering to all of these conditions (see Stanier 1947 for useful discussion) in screening our isolates caused us initially to miss observing the diagnostically critical (Stanier 1947 and Lautrop 1965) gliding motility in many of our cultures.

Flagella were demonstrated by the method of Leifson (1951) and Blenden and Goldberg (1965) and also by the electron microscope method of Baillie et al. (1962) to aid in the interpretation of the flagella stains (Hodgkiss 1960) as well as to show other useful morphological features of the cells.

Concerning microcysts, the media of Dworkin and Voelz (1962) and Dworkin and Gibson (1964) were used to examine cultures of myxobacters for their ability to form microcysts.

The biochemical characteristics studied were as follows.

Amino Acid Breakdown

The Manchester qualitative technique of Sherris et al. (1959) was employed, except that the peptone was reduced to 0.02% to reduce interference by alkaline degradation products from peptone (Thornley 1960). For example, it was found that in Decarboxylase Medium Base containing 0.5% peptone, many organisms produced a strongly alkaline reaction in both test and control tubes. Cultures giving a reading of *p*H 7.2 or higher were considered positive. Substrates used were arginine and ornithine.

Carbohydrate Breakdown

(*a*) *Fermentation in broth* — Organisms were inoculated in Purple Broth Base, to which was added aseptically a filter-sterilized carbohydrate solution to give a final concentration of 1% (w/v) substrate. Tubes were read daily and incubated for at least 17 days before being discarded. The following carbohydrates were

[4]Difco Laboratories Inc., Detroit, Michigan, suppliers of "Bacto" products.

tested: cellobiose, galactose, glucose, lactose, maltose, mannitol, rhamnose, sorbitol, and sucrose.

(*b*) *O/F Test* (Hugh and Leifson 1953) — Negative tubes were incubated for 20 days before discarding.

(*c*) *Cellulase* — Sterile filter paper strips were placed on agar containing 0.25% tryptone and 0.1% yeast extract, and the surface was inoculated. Similar strips were suspended in tubes of medium composed of $NH_4H_2PO_4$ 1.0 g; NaCl 5.0 g; $MgSO_4 \cdot 7H_2O$ 0.2 g; K_2HPO_4 1.0 g; KNO_3 1.5 g; yeast extract 0.1 g; tap water to 1 liter (*p*H 7.0). The inoculated tubes were observed for 16 days. All strips were examined under low magnification for signs of digestion.

Chitinase — Organisms were first inoculated into broth composed of 0.3% beef extract, 0.5% tryptone, 0.01% glucose, and 1.2% chitin in distilled water at final *p*H 7.2. After a 10-day incubation period, the cultures were streaked on agar plates of the above medium. Clear areas around the growth were considered a positive indication of chitinase activity. Chitin[5] was prepared for use according to the method of Hock (1940).

Citrate utilization — Simmons Citrate agar slants were incubated for at least 10 days. All positive cultures were subcultured to eliminate interference from carried-over nutrients.

Fluorescent pigments — Organisms were grown on Pseudomonas F and P agars and on King's Media A and B (King et al. 1954), and examined daily under ultraviolet light for 7 days.

Gelatinase — Tubes of Nutrient Gelatin were used.

Indole formation — Tested after 24- and 48-hr growth in a medium consisting of 1% trypticase[6] and 1% tryptone.

Lecithovitellin reaction — Plates of egg yolk medium were observed for at least 7 days for the appearance of the lecithinase-associated opaque precipitate around the growth.

MR-VP (methyl red, Voges-Proskauer reaction) — Tested in MR-VP medium after 5 days incubation using Barritt's reagents.

Oxidase — According to Kovacs (1956).

Salt tolerance — Nutrient Broth containing 3.5% (w/v) NaCl was heavily inoculated from TGE agar slants and observed for 10–12 days.

Sensitivity to vibriostat 0/129 (2,4-diamino-6,7-di-*iso*propyl pteridine) — Used to detect vibrios according to the method of Shewan et al. (1954) except that the filter paper discs were impregnated with a reagent grade acetone solution of 0.1% (w/v) 0/129 (Bain and Shewan 1968), and when dry, placed on seeded TGE agar.

Violacein pigment — Purple colonies were tested for the presence of violacein, which has the following characteristic properties: insolubility in water and chloroform, solubility in 95% ethanol, produces a green color in dilute H_2SO_4, and produces a green then red color in 10% NaOH (Sneath 1960).

Gluconate oxidation, hydrogen sulfide production, "levan" formation, lipase (tributyrin substrate only), reaction in peptone water, and starch hydrolysis tests were all performed according to Bullock et al. (1965).

2,3-Butanediol and/or acetoin were detected according to Bullock (1961).

Results

An indication of the distribution and morphological types of bacteria, along with detritus, found on the surface of eggs is given in Fig. 3. Some of these bacteria appeared to be sessile, but as a group, they can best be described as "Aufwuchs" or "periphytic bacteria" (Cooke 1956). It was surprising that there were no Protozoa found on the surface of eggs carefully removed from egg holders in the stream, because these organisms are often found browsing on the surface of other incubating fish eggs (G. R. Bell unpublished observations). In contrast, it is not surprising that molds seldom grew on the plate-count medium, because it did not provide favourable conditions. The fact that colonies appeared on eggs (Fig. 3B) suggests that bacteria were actually proliferating on the surface. When eggs died, they soon became almost solidly coated with a great variety of bacteria, many of which we found to be *Pseudomonas* spp. (Fig. 3D and Table 3). It is tentatively suggested that the heavy ($\geqslant 4 \times 10^6/mm^2$ at times) bacterial growth was the result, rather than the cause, of the death of the egg, and that this growth was stimulated by nutrients leaching from the dead egg.

Usually, but not at every sampling, plates made from egg washings were characteristic and readily distinguishable from comparable plates made from river water and from spheres. They were distinguished by means of the predominant, flat, yellow, translucent, spreading, or entire colonies, which subsequently proved to be *Cytophaga* spp. This situation appeared to be true at all stages of embryonic development. The proportion of these colonies varied from 30 to 75%. Plates of water and of spheres had more varied populations consisting of white and yellow mucoid colonies; mauve, mucoid or sometimes crinkled colonies; and light pink colonies. Again, *Cytophaga* spp. usually predominated when eggs were incubated in the gravel in permeable plastic containers.

[5]Nutritional Biochemicals, Cleveland, Ohio.

[6]Baltimore Biological Laboratories Inc., Baltimore, Maryland.

Estimates of Bacterial Populations

Table 1 shows the numbers of bacteria, as calculated from the colony count or "standard plate count at 25 C," found associated with eggs, and with spheres, and in the waters of the Qualicum River and Robertson Creek. These figures are likely to be lower than the "total count" by $10–10^4$ times. The reasons for this discrepancy and the limitations and merits of direct counts compared to colony counts were thoroughly discussed by Collins (1963). At any sampling there was a wide range in values of counts from replicate egg samples, which suggests that at least some of the colonization or association was fortuitous. Potter (1964) also found considerable variation in the bacterial Aufwuchs, but she examined stones and emergent plants in a lake. There appeared to be no consistent relation between the calculated counts on the eggs, on the spheres, and in the water. The temporal fluctuation in counts shown in Table 1 has also been observed by Graham and Young (1934) in lake waters. The aquatic microflora according to most accounts (see Potter 1964), including ours, seems to be quantitatively and qualitatively variable under natural conditions. Although there are no strictly comparable data, the colony counts of bacteria in the river waters (Table 1) appear to be in the higher part of the range, which one might expect from assessing the rather diffuse literature. Colony counts are not required as a test for potable water by public health agencies and therefore, little information exists on the subject of so-called "total counts."

Characteristics and Identities of Isolates

The sources, some diagnostically important characteristics, and the probable identities of the microorganisms selected for study, are presented in Table 2; Table 3 gives the principal references used to identify the isolates. Certain other features

Table 1. Estimates of bacterial numbers (based on colony counts) associated with incubating chum salmon eggs and with "simulated" eggs and in the stream waters (NS, no sample; surface area, egg, 172 mm²; surface area, spheres, 121 mm²; all means arithmetic).

Estimated degree-days (*C*) of incubation	Water temp (*C*)	No. bacteria on eggs: No. eggs	Range *cells/mm²*	Mean *cells/mm²*	No. bacteria on spheres: No. spheres	Range *cells/mm²*	Mean *cells/mm²*	Mean stream water counts per ml
Qualicum River, Dec. 22, 1965–Mar. 29, 1966								
64	4.0	4	120–1000	370	NS	–	–	640
80	4.0	5	250–980	700	4	500–1400	1300	140
108	4.0	5	140–410	290	5	1900–3600	2800	430
140	4.0	5	160–1800	830	3	1800–2800	2100	1000
164	4.0	4	530–3200	1300	4	450–4600	1800	330
216	4.5	5	30–5900	1300	5	910–1600	1100	270
220	4.0	5	89–1300	810	5	1600–4800	2900	360
279	4.5	2	73–220	150	5	150–1700	770	270
297	4.2	4	89–290	140	5	880–2100	1300	350
342	4.5	5	30–810	240	5	330–970	660	490
450	5.0	5	100–330	200	5	96–2000	780	180
582 (hatching)	6.0	5	100–770	330	5	140–1100	560	260
Qualicum River, Dec. 21, 1966–Mar. 13, 1967								
60	4.0	3	110–360	230	2	310–620	470	680
164	4.7	4	280–530	410	4	1800–8600	4900	810
291	5.2	4	200–420	300	NS	–	–	NS
459 (active, eyed embryos)	5.6	4	84–310	230	NS	–	–	510
Robertson Creek, Dec. 4, 1967–Mar. 8, 1968								
37	4.7	4	100–280	210	4	52–290	230	500
115	3.2	4	1–52	37	4	74–390	250	230
129	3.0	3	390–2100	980	4	250–610	450	2000
180	3.0	4	210–1600	690	4	280–470	360	620
216	3.0	3	150–350	240	4	540–1800	1200	250
275	3.4	4	940–5400	2400	4	310–830	550	480
409 ("eyed" eggs)	4.5	4	420–2700	1700	4	460–2000	1200	460

TABLE 2. Sources of pure cultures: studied and their colony pigments, types of motility, flagellar arrangements, and identities. (Cultures 1–48 were isolated according to Bell (1966), cultures 49–79 according to methods described in this paper. All are from the Qualicum River. Missing numbers are of cultures that died before studies could be completed.) Symbols: +, gliding motility present; –, gliding motility absent; 0, flagellar motility absent.

Culture no.	Source	Motility		Colony pigment (insoluble in water)	Identified as
		Gliding	Flagellar		
1	Water	–	Peritrichous	Purple	*Chromobacterium lividum*
2	"	–	1–3 lateral	Cream	*Pseudomonas* group IV (?)
3	"	–	1–8 polar	Cream	" group II
5	"	–	1–2 lateral	Cream	" sp.[b]
7	"	–	1–5 polar	Cream-yellow	" *fluorescens*
8	"	–	1–10 polar	Cream	" "
11	"	+	0	Yellow	*Cytophaga* sp.
14	"	–	1 polar	Cream becoming brown[c]	*Pseudomonas fluorescens*
17	"	–	1 polar	Yellow	*Pseudomonas* group II
18	Live pink egg	–	1–6 polar	Cream	" *putida*
19	"	–	1–6 polar	Cream	" *fluorescens*
20	"	–	1–4 polar	Cream	" group IV
21	Dead pink egg	–	1–8 polar	Cream	" *fluorescens*
22	Dead pink egg	–	1–4 polar	Cream	" "
23	Live pink egg	+	0	Yellow	*Cytophaga* sp.
24	Live pink egg	+	0	Yellow	*Cytophaga* sp.
25	Dead pink egg	–	1–2 polar	Cream	*Pseudomonas fluorescens*
26	Live pink egg	–	1–4 polar	Cream	" "
27	"	–	1–4 polar	Cream	" "
28	"	–	1–2 polar	Yellow	*Pseudomonas* sp.[b]
29	"	+	0	Yellow	*Cytophaga* sp.
30	"	+	0	Yellow	*Cytophaga* sp.
31	"	–	0	Yellow	*Sarcina*
32	Live pink egg	–	1–6 polar	Cream	*Pseudomonas* group II
33	"	–	1 polar	Cream-white	" group II
34	"	–	1 polar	Yellow	" sp.[b]
35	"	+	0	Yellow	*Cytophaga* sp.
36	"	–	1–4 lateral	Purple	*Chromobacterium lividum*
37	Dead pink egg	–	1 polar	Cream	*Pseudomonas* group II
38	Water	–	1 lateral	Cream	Enterobacteriaceae
39	"	–	1 lateral	Cream	Enterobacteriaceae
40	"	–	Peritrichous	Purple	*Chromobacterium lividum*
42	Live pink egg	+	0	Yellow	*Cytophaga* sp.
43	Live pink egg	+	0	Yellow	*Cytophaga* sp.
44	Dead pink egg	–	1–4 polar	Cream	*Pseudomonas fluorescens*
45	Glass sphere	–	1 polar	Cream-purple	*Chromobacterium lividum*
46	Water	–	0	Dark brown[d]	Actinomycete
47	Caddis fly larvae	–	0	Cream	Enterobacteriaceae
48	Caddis fly larvae	–	0	Cream	Enterobacteriaceae
50	Live chum egg	–	1 polar	Cream	*Aeromonas liquefaciens*
51	"	–	1–2 lateral	Cream	Enterobacteriaceae
52	"	–	0	Cream	*Klebsiella*
53	"	–	1 polar	Cream	*Pseudomonas* group II
55	"	+	0	Yellow	*Cytophaga* sp.
56	"	+	0	Yellow	"
57	"	+	0	Yellow	"
58	Polyethylene sphere	–	1–8 polar	White	*Pseudomonas fluorescens*
59	Water	–	1–6 polar	Cream	*Pseudomonas fluorescens*
60	"	–	1 polar	Cream	*Aeromonas liquefaciens*
61	"	–	0	Cream	*Acinetobacter*
62	"	–	Peritrichous	Cream	Enterobacteriaceae

(*Continued*)

TABLE 2. Sources of pure cultures[a] studied and their colony pigments, types of motility, flagellar arrangements, and identities. (Cultures 1–48 were isolated according to Bell (1966), cultures 49–79 according to methods described in this paper. All are from the Qualicum River. Missing numbers are of cultures that died before studies could be completed.) Symbols: +, gliding motility present; –, gliding motility absent; 0, flagellar motility absent.—(*Concluded*)

Culture no.	Source	Motility		Colony pigment (insoluble in water)	Identified as
		Gliding	Flagellar		
63	Polyethylene sphere	–	1 polar	Cream	*Pseudomonas* group IV
64	" "	–	0	Cream	*Acinetobacter*
65	" "	–	+, undetermined	Cream	*Pseudomonas* group II
66	" "	–	1–6 polar	Cream	*Pseudomonas fluorescens*
67	" "	–	1 polar	Cream	*Pseudomonas* group IV
68	Water	–	0	Cream becoming brown[d]	Actinomycete
69	Polyethylene sphere	–	Peritrichous	Cream-purple	*Chromobacterium lividum*
70	Live chum egg	+	0	Yellow	*Cytophaga*
71	Polyethylene sphere	–	1 polar	Cream	*Aeromonas liquefaciens*
72	Live chum egg	+	0	Yellow	*Cytophaga*
73	"	+	0	Yellow	"
74	"	–	0	Pink	"
75	Polyethylene sphere	–	0	Yellow	*Moraxella*
76	Dead chum egg	+	0	Yellow	*Cytophaga* sp.
78	Live chum egg	+	0	Yellow	"
79	Live chum egg	+	0	Yellow	"

[a]Culture no. 31, 46, and 68 were gram-positive, all others were gram-negative rods.
[b]Cf. *P. maltophilia* Stanier et al. (1966).
[c]Noted in some pseudomonads by Stanier et al. (1966).
[d]Water soluble.

TABLE 3. Summary of identities and sources of bacteria isolated, and principal references used for identification.

Identity	No. isolates from:					Total isolates	Principal references
	live eggs	"simulated" eggs	stream water	dead eggs	caddis fly larvae		
Acinetobacter		1	1			2	Baumann et al. 1968b, Thornley 1968
Actinomycete			2			2	Lechevalier 1964
Aeromonas	1	1	1			3	Ewing et al. 1961, Eddy and Carpenter 1964, Bain and Shewan 1968
Chromobacterium	1	2	2			5	Sneath 1966
Cytophaga	16		1	1		18	Stanier 1942, Lautrop 1965, Hendrie et al. 1968, Mitchell et al. 1969
Enterobacter	1		3			4	Hormaeche and Edwards 1960
Enterobacteriaceae					2	2	Breed et al. 1957, Carpenter et al. 1966, Hendrie et al. 1968
Klebsiella	1					1	Hormaeche and Edwards 1960
Moraxella		1				1	Baumann et al. 1968a
Pseudomonas	10	5	8	5		28	Hendrie et al. 1964, Stanier et al. 1966, Hendrie and Shewan 1966
Sarcina	1					1	Breed et al. 1957
Total	31	10	18	6	2	67	

of the isolates are given in the text below. (More detailed descriptions of the cultures can be obtained by writing to G. R. Bell.)

Pseudomonas SPP.

Twenty-five isolates had characteristics that would, according to the scheme of Hendrie et al. (1964) identify them as belonging to the genus *Pseudomonas*. That is, they were gram-negative, motile by polar flagella, oxidase-positive, and not fermentative in the medium of Hugh and Leifson (1953), i.e., O/F Medium. Several characteristics were common to all these isolates but in the identification scheme used they could be subdivided into specified groups. The common features were that all were indole, VP, MR, and H_2S negative, and none produced chitinase. All were catalase and lipase positive and with few exceptions, tolerant of 3.5% NaCl.

Fourteen of the isolates could be placed in group I because they produced both an oxidative reaction in Hugh and Leifson's medium and diffusible, fluorescent pigment in King's B medium. All except one strain (no. 18) liquified gelatin and could be considered to be variants of *P. fluorescens*, whereas no. 18 is probably a strain of *P. putida*. All had multitrichous polar flagella, except no. 14, which was monotrichate, and all produced an alkaline reaction in the arginine medium and no change with ornithine. Although our group I pseudomonads consistently demonstrated the ability to break down arginine, in agreement with the results of Sherris et al. (1959), Thornley (1960), and Stanier et al. (1966), we found that the test was unreliable for characterizing other pseudomonads, in contrast to the findings of Thornley (1960). The ability to oxidize gluconate was more common among group I isolates but was surprisingly uncommon among other designated groups. Bullock et al. (1965) found that all 20 oxidative pseudomonads from fish and a salamander could oxidize gluconate.

Seven of the *Pseudomonas* strains that did not produce fluorescent pigment but that were oxidative in Hugh and Leifson's medium were classified as group II strains. Only two strains produced an alkaline reaction in the arginine medium and none caused an alkaline reaction in the ornithine medium.

Four of the *Pseudomonas* strains (no. 2, 20, 63, and 67) produced an alkaline reaction in Hugh and Leifson's medium and no change in the carbohydrate media tested, and were therefore considered to belong to group IV.

In addition to the 25 "typical" *Pseudomonas* isolates above, isolates no. 5, 28, and 34 also possessed polar flagella but were Kovac's oxidase-negative. In this latter respect they resemble strains of *P. maltophilia* (Hugh and Ryschenkow 1961; see also Hendrie et al. 1964). All three were oxidative in their action in Hugh and Leifson's medium. Indole, MR, VP, and H_2S reactions were all negative and none produced urease and chitinase: no. 28 and 34 produced lipase but only 34 produced amylase.

Cytophaga SPP.

One pink (no. 74) and 17 yellow organisms that produced diffuse colonies on media containing low nutrient concentrations were classified as belonging to the genus *Cytophaga*. All showed similar morphology in the optical and electron microscopes (Fig. 4) and showed gliding motility on agar. As a group they were actively proteolytic on gelatin and produced lipase and amylase. Mitchell et al. (1969) found most cytophagas able to hydrolyze starch and this feature was always positive with our isolates.

All were able to lyse washed, autoclaved cells of culture no. 51, but none was able to lyse living cells (no. 42 and 74 were not tested). If they act as scavengers on the egg surface, it is assumed that they attack dead bacterial cells only.

Chromobacterium SPP.

Five isolates (no. 1, 36, 40, 45, and 69) that produced intensely purple-pigmented colonies were identified as strains of *Chromobacterium lividum*. They all failed to grow at 37 C, and all were oxidative with carbohydrates. Three of the strains (no. 1, 36, and 40) produced gelatinase and, except for no. 69, all were proteolytic in milk. However, all the other biochemical reactions were as listed by Sneath (1960). They were difficult to maintain in laboratory media as Sneath (1960) observed, and although culture no. 1 grew well on Oxoid CM3[7] and on Peptone Yeast Iron agar, long-term survival on these media was not tested.

Aeromonas SPP.

Three strains (no. 50, 60, and 71) were identified as belonging to this genus. They were oxidase-positive, motile by a polar flagellum, and fermentative in Hugh and Leifson's medium, and produced gas from carbohydrates. They were indole-positive, MR-negative, and VP-positive, and all liquified gelatin. All three produced amylase

[7]Oxoid Limited, London, England.

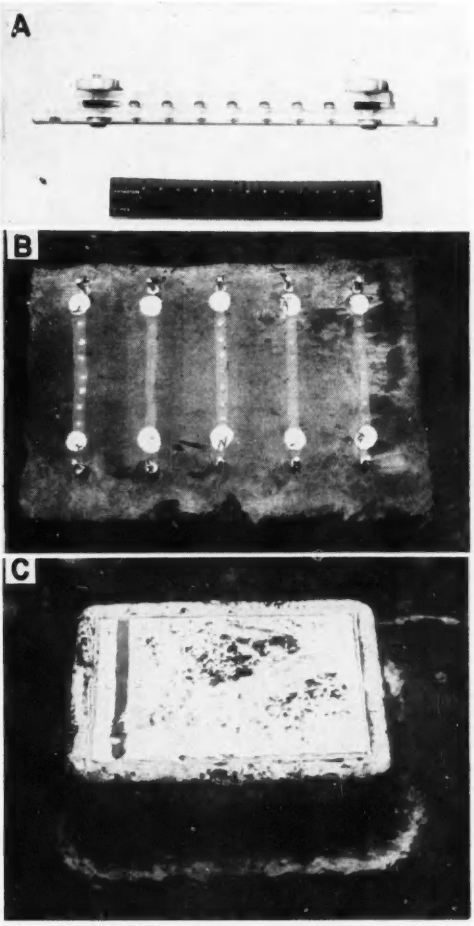

FIG. 1. Apparatus for incubating salmon eggs in the stream and for sampling the eggs with a minimum of contamination: A, the plastic holder or clamp in which the eggs and polyethylene spheres were incubated; B, the holders mounted on stainless steel bolts embedded in a concrete block set on the stream bottom; C, protective plastic cover over the block. Slits on the upstream and downstream ends allowed internal water flow and a hinged aluminum lid facilitated the removal of holders for sampling.

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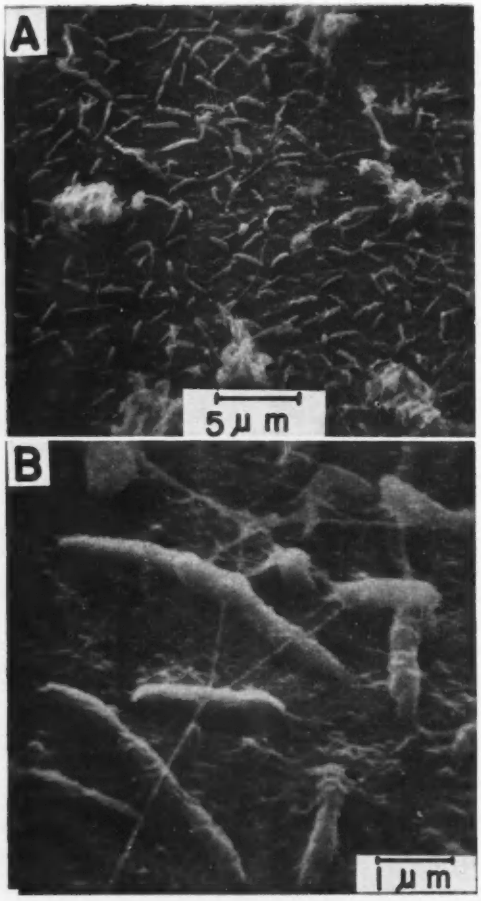

FIG. 2. Scanning electron micrographs of the outermost surface of sockeye salmon eggs from a hatchery tray at the Nanaimo Biological Station: (Shadowed with gold.) A, bacteria appear as rod-shaped bodies scattered like grains of rice; amorphous bodies are probably detritus; B, bacteria on and in a meshlike matrix and attached by weblike material. (Suitable stream-incubating chum and pink eggs were not available to test this new technique, but the results are relevant to this study.)

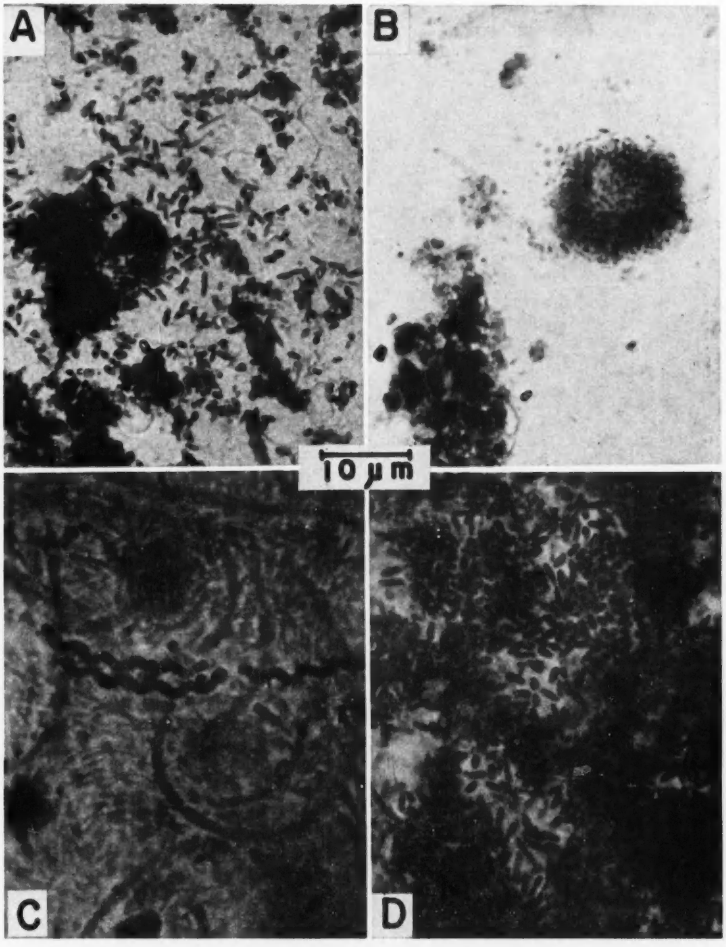

FIG. 3. Fixed and stained (see text for details of method) material on the surface of stream-incubating salmon eggs: A, bacteria and detritus; B, detritus and a colony of bacteria; C, spirochaetes and streptobacilli on an especially heavily populated area. These are examples of organisms that were not isolated by our methods; D, typical growth on a dead egg (lightly populated area selected for photography).

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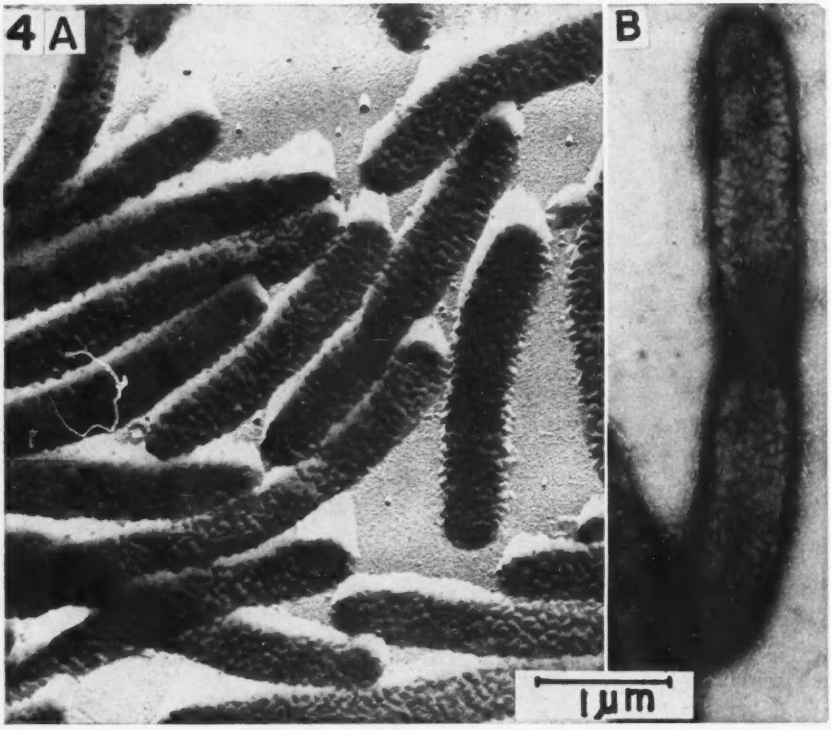

FIG. 4. Electron micrographs of typical cytophagas: A, cells of culture no. 56 shadowed with gold-palladium; B, cells of culture no. 55 negatively stained with ammonium molybdate.

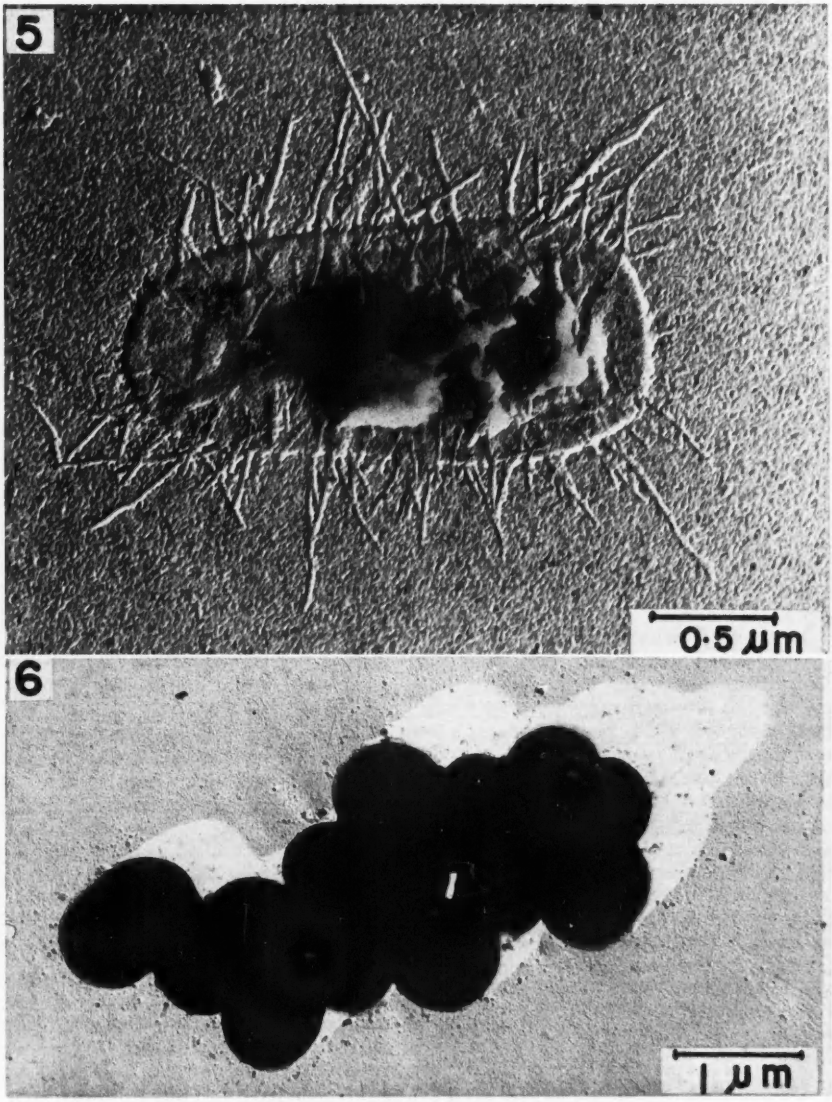

FIG. 5. Electron micrograph of a typical fimbriate cell shadowed with gold-palladium. This example was taken from culture no. 62, which was judged to be an atypical *Enterobacter* sp. Culture no. 51 also contained cells that showed clear fimbriation (nonfimbriate cells occurred in both cultures), but, in addition, the cells were flagellate.

FIG. 6. Electron micrograph of a group of acinetobacters, shadowed with gold-palladium, showing the typical coccoid rods (culture no. 61).

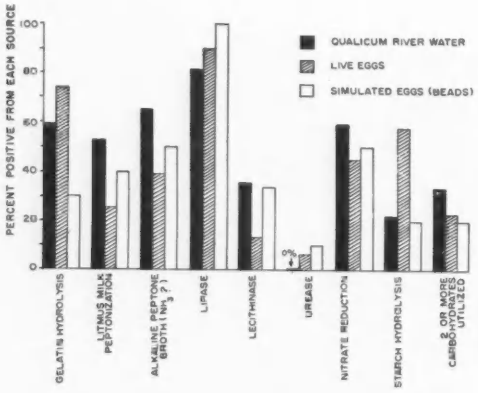

FIG. 7. A comparison of certain biochemical characteristics of bacteria isolated from Qualicum River water, live eggs, and simulated eggs.

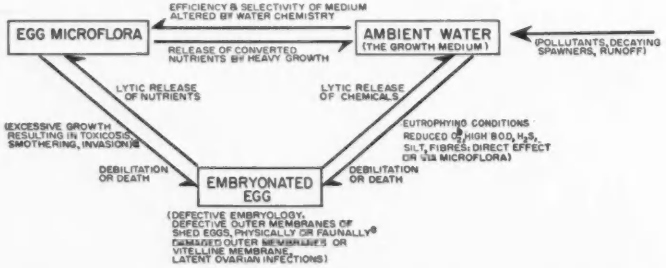
EFFICIENCY & SELECTIVITY OF MEDIUM ALTERED BY WATER CHEMISTRY
EGG MICROFLORA
AMBIENT WATER (THE GROWTH MEDIUM)
(POLLUTANTS, DECAYING SPAWNERS, RUNOFF)
RELEASE OF CONVERTED NUTRIENTS BY HEAVY GROWTH
LYTIC RELEASE OF NUTRIENTS
LYTIC RELEASE OF CHEMICALS
(EXCESSIVE GROWTH RESULTING IN TOXICOSIS, SMOTHERING, INVASION)
EUTROPHYING CONDITIONS
REDUCED O_2, HIGH BOD, H_2S, SILT, FIBRES: DIRECT EFFECT (OR VIA MICROFLORA)
DEBILITATION OR DEATH
DEBILITATION OR DEATH
EMBRYONATED EGG
(DEFECTIVE EMBRYOLOGY, DEFECTIVE OUTER MEMBRANES OF SHED EGGS, PHYSICALLY OR FAUNALLY DAMAGED OUTER MEMBRANES OR VITELLINE MEMBRANE, LATENT OVARIAN INFECTIONS)

FIG. 8. Some interacting conditions and factors within the egg ecosystem, which could result in the death of the egg. *a*, Toxins likely to be continuously removed by flowing waters, but opposed to this, Terner (1968) found that the embryonated egg showed active uptake of some exogenous nutrients: HCN not produced by *C. lividum* but it can be by other chromobacteria (Sneath 1956); *b*, wood bark, for example, killed eggs in this manner (Servizi et al. 1970); *c*, Claire and Phillips (1968) observed stoneflies (*Acroneuria pacifica*) puncturing steelhead eggs in aquaria.

and chitinase but only no. 62 was lipase-positive. They were considered to be strains of *A. liquefaciens*, a facultative pathogen of fishes (Bullock 1961).

Bain and Shewan (1968) and Park and Holding (1966) scored *Aeromonas* spp. as uniformly positive for arginine breakdown but we did not find this so, nor did Ewing et al. (1961) and Popoff (1969). One possible explanation of this apparent discrepancy is that the frequency of positive results depends upon the method used to detect arginine breakdown (Popoff 1969).

Fimbriae, commonly but not exclusively associated with the family Enterobacteriaceae, were observed on a few cells in preparations from culture 60. Tweedy et al. (1968) showed that about 10% of cells from cultures of *A. liquefaciens*, *P. multivorans*, *E. coli*, and a *Vibrio* sp. had fimbriae.

ENTEROBACTERIACEAE

Seven isolates were considered to be members of the family Enterobacteriaceae because they were oxidase-negative and fermentative in Hugh and Leifson's medium. The four motile strains (no. 38, 39, 51, and 62) were probably *Enterobacter* spp., whereas the nonmotile isolate, no. 52, was probably a *Klebsiella* sp. The identities of the other nonmotile cultures (no. 47 and 48) are uncertain. These cultures were isolated from (aseptically washed and homogenized) caddis fly larvae (Bell 1966), insects that are commonly found associated with redds (Astafyeva 1964) and sometimes on the egg itself. The generally unusual nature of these last two isolates, which grew poorly on common laboratory media, suggests that they could have been part of the internal, commensal, or symbiotic microflora of the larvae.

Fimbriae were detected on cells from cultures 51 and 62 (Fig. 5) but not on those from other members of the Enterobacteriaceae.

Acinetobacter AND *Moraxella* SPP.

Two isolates (no. 61 and 64) were identified as *Acinetobacter* spp. (Fig. 6) and one (no. 75) as a *Moraxella* sp. Morphologically, the three cultures were short coccoid rods, which were nonmotile and had no action in carbohydrate media. All were lipase-positive but otherwise were typically nonreactive in the other tests used.

The frequencies of selection, in relation to source, of all the genera and groups cultured are given in Table 3.

BIOCHEMICAL ACTIVITIES OF THE ISOLATES

The most common biochemical characteristic of the bacteria isolated from various sources was the ability to degrade tributyrin (lipase activity), followed by the ability to reduce nitrates and to degrade proteins such as gelatin and casein. No isolate could degrade cellulose, and urease and H_2S producers were comparatively rare. The preponderance of starch hydrolyzers on live eggs was, of course, related to the preponderance of *Cytophaga* spp. thereon. Examination of further data showed that the percentage of pseudomonads from various sources able to liquefy gelatin and to oxidize gluconate increased in the following order: spheres, dead eggs, live eggs, and river water. The highest percentage of *Pseudomonas fluorescens* types was isolated from dead eggs. In general, the pseudomonads from polyethylene spheres appeared to be the least biochemically active.

No further observations can be made on the distribution of biochemical activities in relation to source of the cultures because, as Potter and Baker (1956) commented, there is insufficient information available about environmental factors that influence aquatic microbial populations to make meaningful comparisons.

Discussion

Obtaining accurate bacterial counts of natural populations by the methods presently available is impossible, and many published conclusions have been based on estimates of dubious accuracy. Accordingly, we have drawn few conclusions from the data in Table 1. Apart from inherent technical difficulties of enumerating bacteria, there is the often great difference in numbers of microorganisms occurring at any one time between regions of a body of water — differences that can be greater than those between numbers in an oligotrophic and a eutrophic lake (Potter and Baker 1956). Moreover, all laboratory media, and their methods of incubation, are selective to some degree, and it is obvious that in this work we failed to culture, for example, some species that occurred on the eggs (see Fig. 3C). On the other hand, there was no striking difference between the colony types that occurred on plates made from eggs incubated in plastic tubes (Bell 1966) and those incubated in the more convenient and reliable plastic clamps, and we therefore consider that the more unnatural clamps were providing microbiologically realistic conditions.

Except for one value in Table 1, the counts on the polyethylene spheres (simulated egg surface) incubated in the Qualicum River were consistently higher than those on the eggs. Almost the opposite was true in Robertson Creek, thus apparently countering the explanation that the bacteria were

more readily removed from the spheres. Although no plausible explanation can be offered for this apparent difference between the two streams, it is relevant to note that Collins (1963) suggested from her data that "the surface properties of polyethylene, and nylon in particular, facilitate the supply of something the bacteria need ..." Hence, the spheres used in this work did not offer a chemically inert surface — probably no such thing exists for aquatic bacteria — but probably they did provide a useful, realistic basis for quantitative and qualitative comparison of the microflora. The stimulating effect of polyethylene is further suggested by the fact that in previous work (Bell 1966), which is not strictly comparable, the upper level for etched glass spheres was found to be only 22 bacteria/mm^2; estimates for the living egg were 5–1200/mm^2 and for the water, 10–150/ml.

Many studies on aquatic microbial ecology have failed to distinguish between colonization on any surface and colonization on a particular surface; that is, between "blind" or chance colonization and host- or surface-selected colonization. The propensity of many aquatic bacteria to make use of solid surfaces has been thoroughly discussed by ZoBell (1943) and Cooke (1956). There does not appear to be any quantitative indication that the chum egg surface offers particularly stimulating conditions compared to the polyethylene spheres. But it is possible that many eggs and spheres might have been completely covered by a monolayer of bacteria, if it is assumed initially that all colonies counted came from bacteria on the surface and that colony counts were, conservatively, 10^2 lower than the actual values. This would give 10^5 cells/mm^2, which is roughly the theoretical maximum, if it is further assumed that an average bacterial cell in this study covers 4 μm^2. As a general comparison, Potter (1964) obtained the following orders of bacterial counts per mm^2 on the surfaces of plants (10–10^2), stones (10^2–10^4), and fish (10–10^3) in different lakes. Using sea water, ZoBell and Anderson (1936) found 31×10^3 bacteria/ml and an equivalent of 84×10^3 bacteria/ml attached to the glass of a vessel. The ratio was increased to 10:1 at times and ZoBell (1943 p. 48) suggested that "the bacteria are multiplying on the glass or that the attachment of bacteria promotes the attachment of additional bacteria. Probably adhesive films formed by the first sessile bacteria help other bacteria which come in contact with the surface to gain lodgement long enough to produce their own holdfasts." But superimposed on this adhesive type of colonization is the selective or inducing effect of secretions ("liberations," to be noncommittal) from the egg of such compounds as ammonia (Smith 1947), which could create an oosphere or egg ecosystem.

In agreement with the results of other studies on aquatic bacteriology, almost all our isolates were gram-negative rods. For example, of approximately 1000 cultures isolated by Collins (1963) in the English Lake District, 95% were gram-negative rods. Fewer than 1% of coccus forms were isolated and "spore formers did not make up more than 10% of the total" (p. 49) — the latter presumably meaning at any one time. There is some possibility that our *Sarcina* isolate was not an air contaminant as previously suggested (Bell 1966) because Potter and Baker (1961) frequently isolated gram-positive cocci. They found that gram-positive spore formers were more numerous in mud than in water and this finding was a basis for suggesting that there are autochthonous planktonic (as contrasted to epipsammic) and benthic bacterial populations. However, Wuhrmann (1964) took the view that most of the bacteria in rivers "are introduced by the washings from soil or with sewage" (p. 169). He suggested "that the term 'water bacteria' has no taxonomic and only a small ecological significance" (p. 172). Although this might be only a problem of semantics (even more so than was involved in the now acceptable term "marine bacterium" (MacLeod and Onofrey 1963)), it is well not to be transfixed by the term "water bacteria" but to regard freshwater bacteria in the context of local or regional ecosystems (Rowe 1961). Possibly there is no more reason to suggest that freshwater bacteria are only displaced soil types than the converse. The fact that we did not isolate any gram-positive spore formers is perhaps indicative of minor soil and mud contamination of the samples, regardless of their source. However, there does not appear to be any generally accepted explanation for the paucity of gram-positive spore formers or indeed of gram-positive bacteria in general, in bodies of fresh water that are in continuous contact with soil.

Collins (1963) remarked that common aquatic bacteria were characterized by their marked lack of biochemical activities, which consequently made them difficult to classify. Although we encountered similar difficulties resulting in a few dubious identifications, it was not our experience that "aquatic" bacteria were particularly inactive. Obviously, living cells of all kinds carry out a vast number of biochemical activities and any apparent lack of activity is probably a reflection of inappropriately formulated test media and insufficiently sensitive detecting methods. Permeability barriers of the cell may also account for some apparent inactivity.

We agree with Bullock et al. (1965) and Stanier et al. (1966) that the O/F Medium of Hugh and Leifson (1953) appeared to give a more sensitive indication of glucose utilization than did the Purple Broth Base, and that the O/F Medium might therefore be an improved base for detecting the breakdown of all the diagnostic sugars. Comparison of the reactions of our isolates in O/F Medium, peptone water, and carbohydrate broth (unpublished observations) suggested that the increased sensitivity of the O/F Medium was not always due exclusively to reduced ammonification by an organism. Perhaps carbohydrate utilization in O/F Medium was stimulated by the presence of certain ions such as phosphate. Since, as Collins (1963) pointed out, some aquatic bacteria are dependent upon solid surfaces for their proliferation, it might also be possible that the semisolid agar of the O/F Medium provides more appropriate growth conditions. In this regard it would be interesting to see if there was improved growth and substrate utilization by some aquatic bacteria in tubes of broth filled with tiny beads (Parr et al. 1963) or packing material from fractionating columns. As a further explanation of apparent limited biochemical activity, it is suggested that for bacteria accustomed to living in very dilute nutrient solutions, the common test media and substrate concentrations may be sublethally toxic.

Perhaps, like Cowan (1970), we might have been more concerned with what the organisms did rather than with giving them a name. But in a real sense these are interconnected and inseparable. Actually, much useful ecologic information could also have been obtained by classifying the isolates into nutritional groups according to the methods that Lochhead (1952) and colleagues used so successfully in studies of the rhizosphere. Another approach might have been to estimate the number of isolates belonging to each of several physiological groupings such as Thibault et al. (1970) did in their ecological study of a trout stream.

Our results suggest that the stream-incubating salmon egg has a characteristic autochthonous microflora in which *Cytophaga* spp. predominate. Dead eggs appear to be populated mostly by fluorescent pseudomonads. It is possible that those eggs that did not have characteristic populations were in a stage of incipient disease, but it is also possible that their populations merely reflected environmental variations. Further work will be necessary to establish if this indigenous microflora is characteristic of all salmonid eggs (compared, for example, to frog or bullhead eggs) in all types of streams. (The bacterial flora at the sampling sites in the Qualicum River and Robertson Creek appeared generally similar.) It was, of course, impossible to separate completely the eggs and spheres from the water in which they were bathed, and from all adhering detritus, so, therefore, some organisms isolated were probably adventitious. However, the cytophagas appeared to be intimately associated with the egg because the proportion of these organisms increased if the egg had first been gently washed aseptically to waste, and then sampled as usual. Pseudomonads, too, were numerically important on incubating eggs and on "simulated" eggs, although the latter appeared to have the more varied population.

The fact that certain bacteria, such as the gliding myxobacters, tend to colonize or become associated with the egg surface (commensal population) suggests that this surface provides unique physical and/or chemical opportunities. Although the fertilized egg might be compared in a general way to the rhizosphere, it does not appear to provide the quantity and array of growth factors and nutrients that the plant root does. According to most accounts (Hayes 1949 and Smith 1957), the developing salmonid embryo utilizes the endogenous nutrients very efficiently, and so there are probably few excreted waste products, except small quantitites of carbon dioxide and ammonia, which diffuse through the external membrane (Smith 1947). Smith's figures are open to question because he did not appear to control or account for the possible effects of commensal microfloras on the type and amount of nitrogenous excretory products. (A similar criticism might apply to some of the work of Terner (1968)). However, as previously observed (Bell 1966), the paucity of urease-positive isolates associated with the egg surface suggests that urea does not diffuse as such through the radiate membrane. The carbon dioxide evolved is unlikely to stimulate growth because the water is probably already saturated with this gas.

Before discussing the possible role of bacteria in disease and death of stream-incubating salmon eggs, it would be well to set the problem within the framework of modern views on the germ theory of disease so lucidly expressed by Dubos (1955) and related to fish by Snieszko (1964). The classic and seductively reasonable "germ theory of disease," which holds that when a virulent microbe reaches a susceptible — not necessarily debilitated — host, disease ensues, is now considered so oversimplified that it rarely fits the facts of disease processes. "There are many situations in which the microbe is a constant and ubiquitous component of the environment but causes disease only when some weakening of the patient by another factor allows infection to proceed unrestrained, at least for

a while. Theories of disease must account for the surprising fact that, in any community, a large percentage of healthy and normal individuals continually harbor potentially pathogenic microbes without suffering any symptoms or lesions" (Dubos 1955 p. 32). In other words, clear-cut distinctions between pathogens and nonpathogens are often difficult to make, although there are organisms that fall at either end of the spectrum of pathogenicity. Snieszko (1964) distinguished obligate pathogens (e.g., *A. salmonicida*, *H. piscium*) from facultative pathogens (e.g., *A. liquefaciens*, *P. fluorescens*, myxobacters), but this should not be thought of as a rigid dichotomy. Most fish diseases are caused by bacteria in the latter group, and there seems little reason to doubt that this is also true for fish eggs.

Even though we have not deliberately looked for egg pathogens, being primarily concerned with the microflora of healthy eggs, it does not seem likely that bacteria will be found as primary invaders or pathogens of healthy, naturally incubating salmon eggs. At this stage of our investigation, the evidence for this statement is partly circumstantial and partly documented. However, in apparent contrast to this view, Oppenheimer (1955) and Shelbourne (1965) found that antibiotics that reduced the numbers of bacteria in their tanks of sea water increased egg survival significantly. But under their artificial conditions, which are notorious for stimulating unnaturally heavy growth of microorganisms on surfaces, bacteria could be directly involved in causing egg mortalities. Also, the antibiotics could have protected any abnormal, sublethally damaged or debilitated eggs — fragile at best — from bacterial invasion. (Often a substantial percentage failed to hatch even in antibiotic-treated water, suggesting that other factors also play a role.) And finally, it should be asked, particularly regarding Shelbourne's results, why, if one postulates the existence of obligate pathogens of eggs, did about half the plaice (*Pleuronectes*) eggs survive in the untreated tanks? The answer could be "individual resistance," and we have then completed the cyclic argument. In our own work we found that five out of six isolates from dead eggs were apparently common pseudomonads and that shock-killed eggs gradually took on a predominantly pseudomonad microflora. These pseudomonads probably grew in response to the release of amino nitrogen (Smith 1947) or exosmotic products (Gray 1932) from the autolyzing egg. Again, if these pseudomonads were pathogens and a constant component of the environment, why were all the eggs in the stream not killed? Further, if any stream bacteria were able to utilize, vigorously, components of the outer membrane, these organisms would be selectively cultured on all eggs and there would be no surviving eggs. The outer membrane must be highly refractory to many agents because substantial pieces can be found in the gravel months after hatching (McNeil et al. 1964; G. R. Bell personal observations). (The remarkable "hatching enzyme" (Hayes 1949; Bell et al. 1969) is the only known agent that can rapidly dissolve under natural conditions the outer membrane of the incubating salmon egg.) It is possible that microorganisms that have the potential to physically (e.g., a spirochaete) or enzymatically (e.g., pronase (Bell et al. 1969)) penetrate the outer membrane do exist, but these might be prevented by other microorganisms or other factors from colonizing the healthy egg. In rare instances bacteria might penetrate via the micropyle just before, or coincident with, fertilization, and since we could not detect in vitro any antibacterial activity in the perivitellin fluid, the invading organism might proliferate and kill the egg. (The possibility of bacteria existing inside newly shed, apparently healthy eggs, needs investigation.) Some fertilized eggs may also die because of inherent structural or embryological defects, which, although physiologically tolerable for various periods of time, make them vulnerable to bacterial pathogenesis. For example, there is a thin (ca. 0.5–1.5 μm) physically and chemically distinct outermost covering on the zona radiata, designated membrane B by Bell et al. (1969) but which is probably identical to the "zona radiata externa" of Flügel (1967). Imperfections of this layer might render the principal membrane less durable or permit microbial invasion via unplugged pore canals.

Future research should be directed toward (*a*) raising bacteriologically sterile eggs — which we have tried with limited success — in order to test the pathogenicity of cultures; (*b*) examining, microbiologically, the contents of live and recently dead eggs; (*c*) examining, histologically, the zona radiata of recently dead eggs; (*d*) developing microtechniques for injecting bacteria into eggs and (*e*) searching for microorganisms that can digest the ichthulokeratin (Young and Smith 1956) of the radiate membrane.

In summary, the healthy salmon egg is part of a dynamic ecosystem in which the developing embryo is protected from microbial influence or invasion by a thick (40–70 μm), semipermeable, physically and chemically durable keratinoid outer membrane. It is suggested that physical and chemical conditions in the environment are probably the most crucial factors governing egg survival in nature, but that death is probably the result of

complex interactions such as those summarized in Fig. 8.

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New Distribution Records of Reptant Decapod Crustacea, Including Descriptions of Three New Species of *Pagurus*, from the Waters Adjacent to British Columbia

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HART, J. F. L. 1971. New distribution records of reptant decapod Crustacea, including descriptions of three new species of *Pagurus*, from the waters adjacent to British Columbia. J. Fish. Res. Bd. Canada 28: 1527–1544.

Three hermit crabs, *Pagurus caurinus*, *P. quaylei*, and *P. stevensae*, from British Columbia are described as new. *Calastacus quinqueseriatus* Rathbun, *Paguristes ulreyi* Schmitt, *Pagurus cavimanus* (Miers), *P. samuelis* (Stimpson), *Parapagurus pilosimanus* Smith, *Munidopsis quadrata* Faxon, and *Chionoecetes tanneri* Rathbun have not been recorded from the area between 48° and 55°N and 123° and 135°W, and also show considerable extensions of the known ranges. Within the confines of the same area, *Callianassa gigas* Dana, *Paguristes turgidus* (Stimpson), *Pagurus cornutus* (Benedict), *P. hemphilli* (Benedict), *Orthopagurus minimus* (Holmes), *Petrolisthes cinctipes* (Randall), *Scleroplax granulata* Rathbun, *Pinnotheres pugettensis* Holmes, *P. taylori* Rathbun, and *Planes marinus* Rathbun are reported with extensions to known ranges. *Pagurus capillatus* (Benedict), *P. tanneri* (Benedict), *Paralomis verrilli* (Benedict), and *Lithodes couesi* Benedict are recorded, apparently for the first time from British Columbia, although known from both north and south of this area.

HART, J. F. L. 1971. New distribution records of reptant decapod Crustacea, including descriptions of three new species of *Pagurus*, from the waters adjacent to British Columbia. J. Fish. Res. Bd. Canada 28: 1527–1544.

Trois nouvelles espèces de pagures, *Pagurus caurinus*, *P. quaylei* et *P. stevensae*, provenant de la Colombie britanniqûe, sont décrites. *Calastacus quinqueseriatus* Rathbun, *Paguristes ulreyi* Schmitt, *Pagurus cavimanus* (Miers), *P. samuelis* (Stimpson), *Parapagurus pilosimanus* Smith, *Munidopsis quadrata* Faxon et *Chionoecetes tanneri* Rathbun n'ont pas encore été signalés dans la zone comprise entre les latitudes 48° et 55° nord et les longitudes 123° et 135° ouest. L'aire de répartition de ces espèces se trouve considérablement agrandie. L'auteur mentionne la présence, dans les mêmes limites, de *Callianassa gigas* Dana, *Paguristes turgidus* (Stimpson), *Pagurus cornutus* (Benedict), *P. hemphilli* (Benedict), *Orthopagurus minimus* (Holmes), *Petrolisthes cinctipes* (Randall), *Scleroplax granulata* Rathbun, *Pinnotheres pugettensis* Holmes, *P. taylori* Rathbun et *Planes marinus* Rathbun en des endroits où ces expèces n'avaient pas encore été signalées. Enfin il rapporte, apparemment pour la première fois, la présence de *Pagurus capillatus* (Benedict), *P. tanneri* (Benedict), *Paralomis verrilli* (Benedict) et *Lithodes couesi* Benedict dans les eaux de la Colombie britannique, bien que ces espèces aient été signalées tant au nord qu'au sud de cette zone.

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WHILE working through collections of reptant decapod Crustacea taken from the waters off British Columbia, I have found a number of species that appear to be undescribed, or that have not been recorded for this area, or that provide northern or southern extensions of the known range. The area under study is roughly between 48° and 55°N and 123° and 135°W.

Descriptions of New Species

Both *Pagurus caurinus* and *P. quaylei*, which are here described as apparently unrecorded in the literature, would appear to belong to the group of *Pagurus* recently designated as "groupe I (groupe *miamensis*)" by Forest and Saint Laurent (1967). Species included in this group have the frontal margin of the carapace obtuse and somewhat protuberant. The eyestalks are subcylindrical and

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rather slender and the eye scales are large, with the extremities either uni- or multi-dentate. Chelipeds are very unequal in size and the hands are covered with spiny tubercles and numerous setae. The length of the carapace does not exceed 8 mm. The members of this group are usually found in the lower intertidal or the upper subtidal zones of warm or temperate seas. Some individuals of *P. caurinus* do attain a greater size than the species originally placed in this group and a few of both the species dealt with here have been taken in deeper water (126 m).

The holotypes, all males, of the three new species are deposited in the Provincial Museum of British Columbia and paratypes are to be distributed elsewhere.

Initials are used in the tables of material examined and in the new records for the chief collectors: D. B. Quayle, T. H. Butler, and J. F. L. Hart. In the tables also, the Fisheries Research Board of Canada is designated by FRB and the Allan Hancock Foundation stations Velero III and Velero IV by V-3 and V-4. Subtidal is for collections from less than 10 m depth. Ovigerous females are indicated by ♀♀.

The descriptions of the colouring of the living animals result from examination under magnification and so greater detail of colour pattern may be given than can be easily discerned with the naked eye. The term *stripe* is used to designate a streak of colour running parallel to the longitudinal axis of the body or of the appendage. *Band* refers to a stripe of colour running around or across the body or appendage.

Certain descriptive terms are used to describe the morphology of the hermit crabs. *Shield* refers to the calcified dorsal part of the carapace anterior to the cervical groove. *Seta*, *hair*, or *bristle* are used for the fine cylindrical exoskeletal outgrowths, and are usually pliable, whereas *spine* is rigid and often a corneus process. When a spine is laterally flattened and/or wide, it may be referred to as a *tooth*. Small *knobs* on the surface are often called *granules* when dorsally flattened or rounded, and *tubercles* when the bases are rounded, the tips cone-shaped and sharp-pointed, with or without corneus tips.

Rhizocephalan parasites occurred in less than 5% of each of the three new species examined. The majority of these were of the *Peltogasterella* type and attached to the abdomen. The remainder were of the *Thompsonia* type, which occurred on various parts of the thorax and appendages.

In the figures, magnifications are indicated by lines representing 5 mm in Fig. 1, 8, and 17, and 1 mm in the remaining figures.

Pagurus caurinus n.sp.

Fig. 1–7

Pagurus setosus Hart 1940 p. 94 (in part).

Material examined — Table 1.

Description — Carapace shield subequal in length and width. Surface smooth and almost flat, with some patches of short, stiff setae. Rostrum obtuse, covered with a tuft of setae and lateral teeth nearly obsolete. No submarginal teeth. Carapace with long soft setae laterally.

Eyestalk long, slender, and slightly constricted medially. Ophthalmic scale with dorsal surface flat and inner margin curved, tip blunt, and large sharp submarginal tooth.

Antennular peduncle subequal or slightly longer than eyestalk.

Antenna setose, with small sharp tooth on base of peduncle, segment 2 with a small sharp tooth on inner side at base of acicle, another on ventral distal margin and a broad lateral projection with the tip cut into 2 or 3 teeth. Acicle curved and decreasing in width distally, setose, and tipped with a stout spine. Segment 3 short: not reaching end of acicle. Segment 4 nearly twice as long as segment 3 and more slender. Flagellum slightly longer than thoracic appendages and bearing tufts of small setae.

Third maxilliped with crista dentata of ischium serrate with corneus teeth, which decrease in size distally. A large accessory tooth medially.

Right cheliped narrow but deep, with many tufts of long setae around bases of tubercles: setae vary in length and degree of plumoseness and tufts consist of 4 or less setae, seldom of equal length. Ischium short, with few if any, flat granules ventrally. Merus subcylindrical in cross section, subequal in length to carpus but narrower. 1, or occasionally 2 in females, large knobs medio-ventrally, and a row of small tubercles on ventral distal margin. Dorsal distal margin with several small teeth. Carpus subequal in width but shorter than chela. Dorsal surface slightly convex and armed on the inner margin with stout spiny tubercles; dorsal surface with small tubercles and tufts of long setae. Chela slightly convex dorsally: inner margin of propodus straight, and outer curved. Lateral margins of palm and fingers bordered with close-set corneus-tipped tubercles with less distinct rows of tubercles on dorsal surface. Tips of fingers corneus and cutting surfaces with flat interlocking teeth.

Left cheliped slender, setose and reaching to base of dactyl of right. Ischium with small granules on ventral ridge, varying considerably in size and number. Merus like that of right, but without any large median knobs ventrally: outer distal ventral margin usually with several spiny tubercles. Carpus narrow, subequal to merus in length and slightly shorter than chela. Chela with additional 2 or 3 rows of smaller tubercles dorsally. Both fingers with a medial row of tubercles. Fingers corneus-tipped and cutting surfaces with combs of short corneus setae.

Walking legs setose, and those of right side subequal in length or longer than right cheliped. Right 2nd pereiopod with a number of spiny tubercles on dorsal ridge of carpus. Carpus shorter than subequal propodus and dactylus. Propodus with 2 or 3 spines ventrally. Dactylus with stout spines on ventral margin and on upper inner face, which are conspicuous only in large individuals. Terminates in a stout corneus claw, which is slightly twisted. Third pereiopod similar but only one terminal spiny tubercle on carpus. Left pereiopods similar but

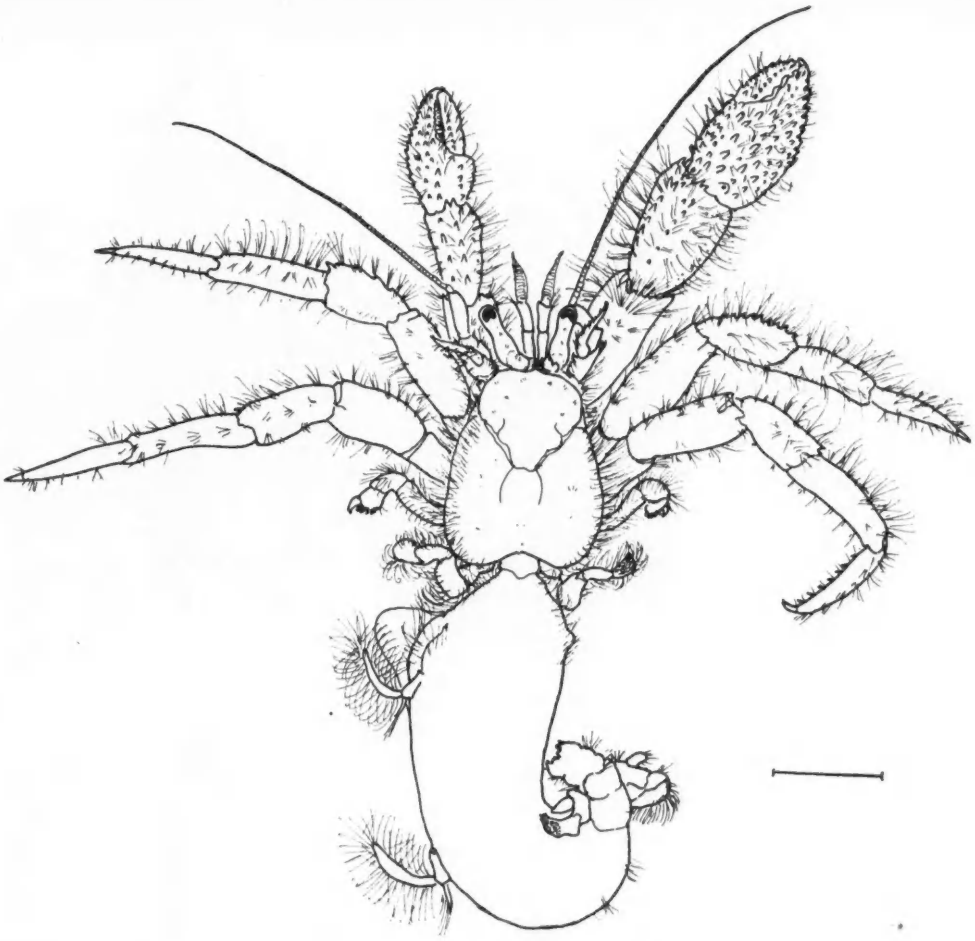
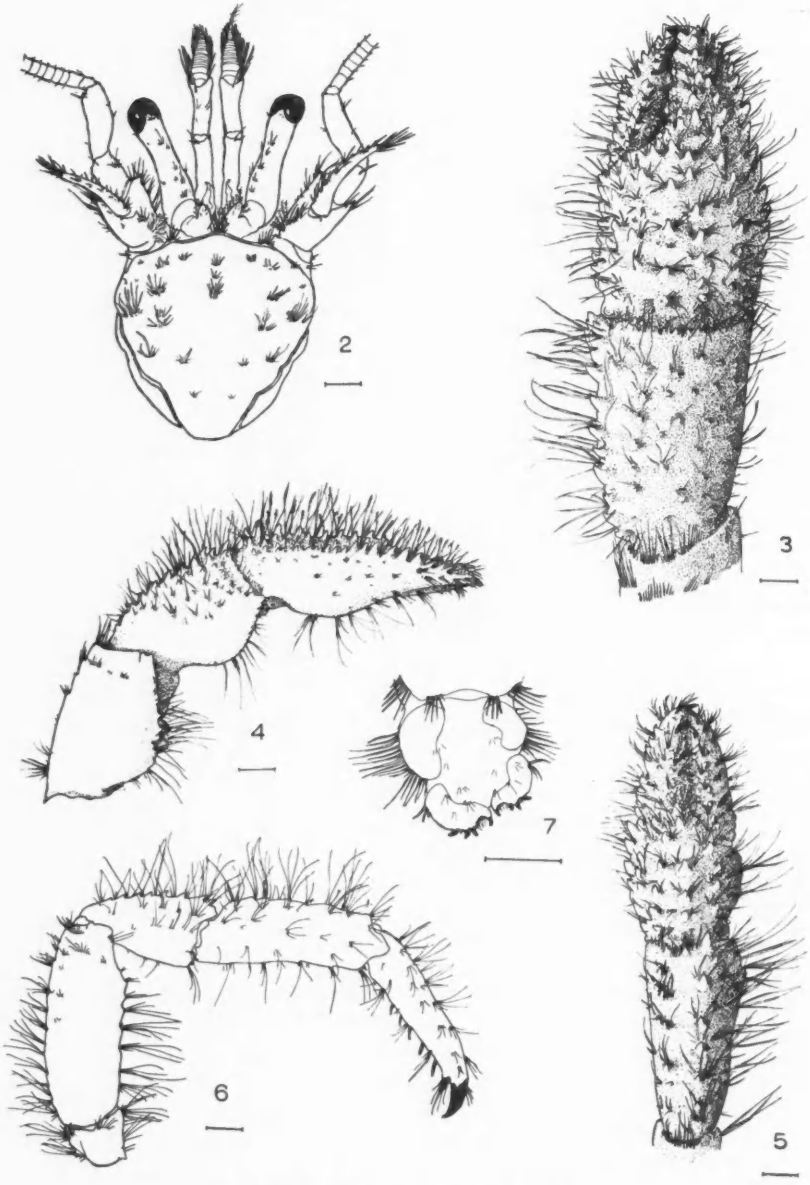


FIG. 1. *Pagurus caurinus* n.sp. Male.

less tubercles on carpus. Fourth and fifth pereiopods very setose.

Telson with anterior and posterior lobes similar in size and shape. Posterior lobes each with 2 or 3 stout curved corneus teeth separated by a concave hiatus from the single large median tooth on either side of the median cleft.

Colour of living animal — Carapace a light grey, with longitudinal stripes of purple and a row of light-coloured spots in each stripe. Laterally, red-brown and cream marbling. Abdomen mottled with grey and purple. Peduncle of both pairs of antennae, eyestalks, and third maxillipeds light coloured with greenish brown bands. Cornea of eye covered with yellow chromatophores, except for narrow bands of black. All flagella orange. Meri of chelipeds a reticulated red-brown and grey, with a dull white or yellowish band on distal part. Carpi of both chelipeds grey-green and red-brown, with tubercles grey based and orange tipped. Chelae light greenish-brown with grey; orange-tipped tubercles and finger tips orange-red. Walking legs with meri red-brown with light spots and a yellowish-white irregular distal band, margined with some orange. Carpus brown with grey spots and median lateral face yellowish. Proximal propodus with a narrow light-coloured band, median part red-brown with grey spots (base of tufts of setae) and distally an opaque white band. Dactylus red-brown with grey spots becoming orange at tip. Claw a translucent brown. The long tan setae mask the colours.



FIGURES 2–7. *Pagurus caurinus* n.sp. Male.

Fig. 2. Shield and head appendages; Fig. 3. Dorsal view, right chela and carpus; Fig. 4. Lateral view, right cheliped; Fig. 5. Left chela and carpus; Fig. 6. Right second pereiopod; Fig. 7. Telson.

TABLE 1. *Pagurus caurinus* n.sp. material examined.

Locality	Depth (*m*)	Bottom	Date	Station	Sex ♂	Sex ♀	Sex ♀♀	Collector
			Alaska					
Kodiak 58°07.8′N, 150°51′W	126	Sand & boulders	31/8/63	FRB 63-74		1		DBQ
			British Columbia					
Yakan Pt. 54°05′N, 131°50′W			27/7/63			3		THB
Masset Beach 54°02′N, 132°10′W	Intertidal		6/65		1			DBQ
Naden Harbour 54°01.2′N, 132°40′W	23	Mud & weed	29/5/65	FRB 65-14	5			DBQ
Port Louis 53°42′N, 132°58′W	Subtidal	Gravel	4/6/69		4		2	JFLH
Houston Stewart Chn. 52°15′N, 131°05′W	Subtidal	Gravel	30/5/69		7		1	JFLH
Restless Bay, Drury Inlet 50°57′N, 126°51′W	Intertidal	Rocky	23/6/70		3			JFLH
Cox Is. 50°47′N, 128°40′W	Subtidal	Sand	25/6/70		1		1	JFLH
Entr. Quatsino Sd. 50°25′N, 128°05′W	Subtidal		27/6/70				1	JFLH
Checleset Bay 50°08′N, 127°45.5′W	44	Coarse gravel	28/6/70	FRB 70-53	15	4	3	JFLH
Checleset Bay 50°03′N, 127°39′W	34	Mud & sand	28/6/70	FRB 70-56	1	2	1	JFLH
Esperanza Inlet 49°45.8′N, 126°56′W	10	Rock	30/6/70	FRB 70-67		2	1	JFLH
Nuchatlitz Inlet 49°45′N, 126°59′W	Subtidal		29/6/70		3			JFLH
Sydney Inlet 49°21.5′N, 126°14.7′W	13	Firm clean sand	30/6/70	FRB 70-70		1	3	JFLH
Departure Bay 49°12′N, 123°54′W	73	Rocks & glass sponges	1/6/33		1			JFLH
49°12′N, 123°58′W		”	16/3/33				1	JFLH
Dodd Narrows 49°08′N, 123°58′W	9		27/7/34		8	1	1	JFLH
Frank Is, Cox Bay, Tofino 49°08′N, 125°55′W	Intertidal	Rocky & weed	10/7/60		14	2	1	
			29/7/61		5			
			1/7/65		35	5	22	
			18/8/66		27	9	12	JFLH
Wickaninnish Bay 49°03′N, 125°46′W	Intertidal	Sand	19/8/66			2		JFLH
Mill Bay, Saanich Inlet 48°30′N, 123°25′W	27	Mud	14/2/68		1	1		JFLH
Botanical Gdns., Port Renfrew 48°30′N, 124°25′W	Intertidal	Rocks	3/5/69		3			A. D. Carl
” ” ”	”	”	4/5/58		4	2	1	JFLH
McNeill Bay, Victoria	”	”	20/7/66		1			JFLH

Juveniles and small individuals (shield 1–1.5 mm in length) differ in that they are transparent, with some red or tan pigment. Meri of pereiopods are dark red and rest of appendage straw coloured with orange tips. Adult colouring is slowly acquired and when the shield is about 2.5 mm the colour pattern is like the adult but the colour is less intense.

Size — Shield length: males 1.4–7 mm, females 1.8–5 mm and ovigerous females 1.8–5 mm.

Range — Vicinity of Kodiak, Alaska (58°07.8′N, 150°51′W) to Victoria, B.C. (48°25′N, 123°22′W). Littoral to 126 m.

Habitat — Low intertidal in some areas on the west coast of Vancouver Island, where small individuals are at the base of eelgrass or kelp. Larger individuals are found in crevices of rocks or under kelp holfasts.

Field recognition — Orange flagella and tips of pereiopods combined with distinct white bands of distal part of propodi of walking legs.

Notes — Ovigerous females have been found from March until August. Some of those found in August had freshly extruded eggs, so the breeding season probably lasts for at least 6 months.

There is considerable variation in the amount of setation on the appendages, as well as the type of setae, which vary in length and also in amount of plumosity and in number. Females appear to have "fuzzy" chelae, but as detritus adheres to the plumose setae, it is difficult to judge the degree.

Four species of *Pagurus* found in British Columbia have often been confused. These are *P. kennerlyi* (Stimpson), *P. setosus* (Benedict), *P. capillatus* (Benedict), and *P. caurinus*.

The length of the antennal acicle has been used as a distinguishing character to separate *P. kennerlyi* from *P. setosus* but this character seems to be reliable only when comparing large specimens. Furthermore, a study of a long series of individuals of *P. caurinus* with shield lengths varying from 1.4 to 7 mm has revealed the gradual growth of the acicle: from not reaching as far as the cornea, to exceeding it in length.

The four species under consideration have spiny tubercles and tufts of long setae on the dorsal surface of the right cheliped. The setae may be all naked or some may be plumose. The colour patterns are somewhat similar in preserved specimens.

However, *P. caurinus* can be distinguished immediately from the other three species by the shape of the posterior margin of the telson. In this species the distal part of the telson is emarginate with three or four large curved teeth on either side of the median cleft, whereas in the others the telson has distally straight margins meeting medially at an angle and armed with numerous straight teeth.

Pagurus caurinus differs also from *P. capillatus* and *P. setosus* by the subequal length of the dactyli and propodi of the walking legs, as compared to the more elongate dactyli of the latter two species. It can be separated from *P. kennerlyi* by the proportionate size of the parts of the right cheliped: in *P. caurinus* the carpus is about the same length as the chela, whereas in *P. kennerlyi*, it is only about one-half as long as the chela.

If the colour pattern is still visible, bands of light and dark pigmented segments of the antennal flagella serve to seperate *P. kennerlyi* from the others, all of which have unicoloured flagella.

The name "*caurinus*" is derived from the Latin "of the northwest wind, northwestern" (Jaeger 1944).

Pagurus quaylei n.sp.

Fig. 8–16

Material examined — Table 2.

Description — Carapace shield subequal in length and width and relatively flat. Smooth and shiny with a few tufts of short setae. Tufts of long soft setae laterally and on branchial region. Rostrum and lateral teeth rounded and without submarginal teeth.

Eyestalk cylindrical and elongated. More than one-half length of shield. Cornea slightly wider than stalk. Ophthalmic scales oval, concave dorsally, with one or more marginal teeth.

Antennule peduncle short, reaching slightly past cornea of eye.

Antenna with basal segment armed with 1 lateral tooth. Second segment stout with 1 tooth at base of acicle, 1 on inner-ventral distal border, and 2–5 on lateral projection. Acicle narrow, slightly curved, with sharp tip and setose on inner margin. Third segment short and fourth twice third. Flagellum longer than chelipeds.

Third maxilliped with crista dentata on ischium composed of small corneus teeth diminishing in size distally and 1 large accessory tooth. 1 or 2 teeth on median margin of basis.

Right cheliped relatively stout with stiff setae in tufts around tubercles. Ischium short, with a few tubercles and tufts of setae on inner and outer ventral lateral margins. Merus smooth dorsally with a few tufts of short setae. No teeth on distal dorsal margin. Ventrally rounded, with 1 large median tubercle and a number of smaller tubercles medially and on the distal margins. Carpus subequal in length, but wider than merus. Inner margin armed with a row of large sharp forward-pointing tubercles. Dorsal surface covered with small spiny tubercles in irregular rows and surrounded by tufts of setae.

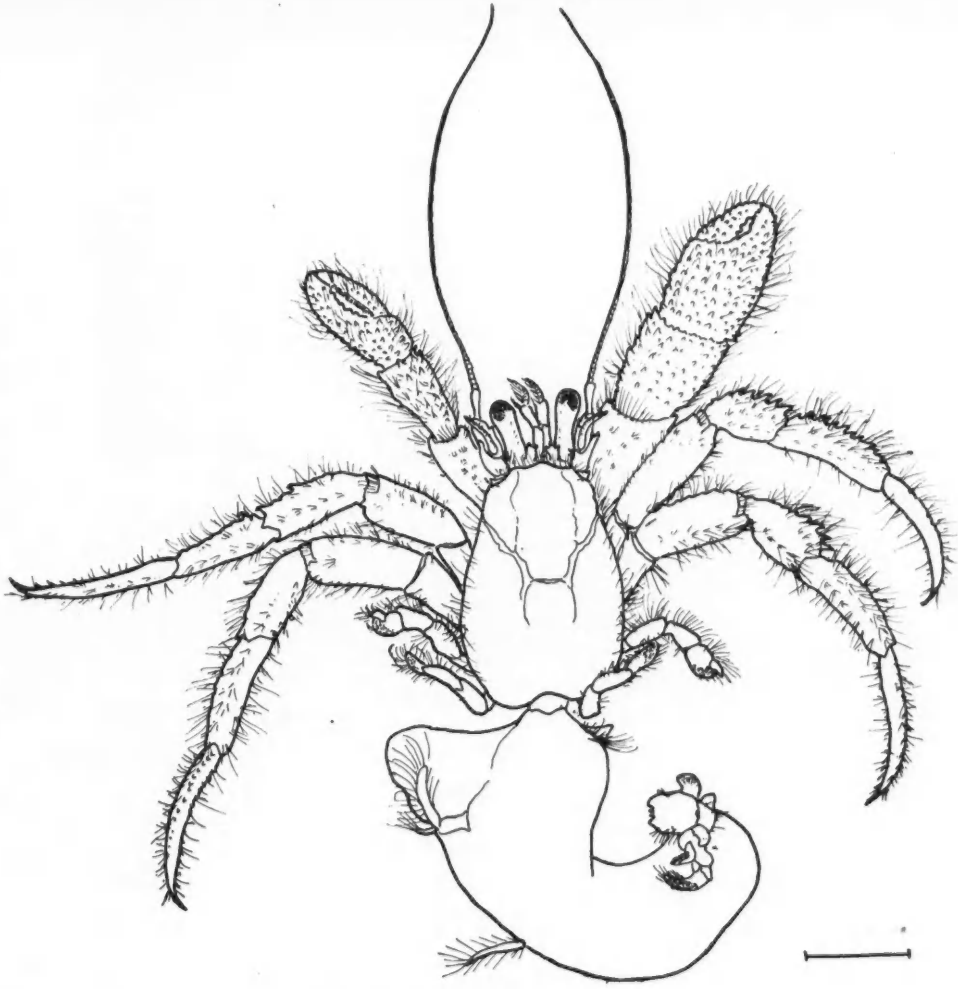
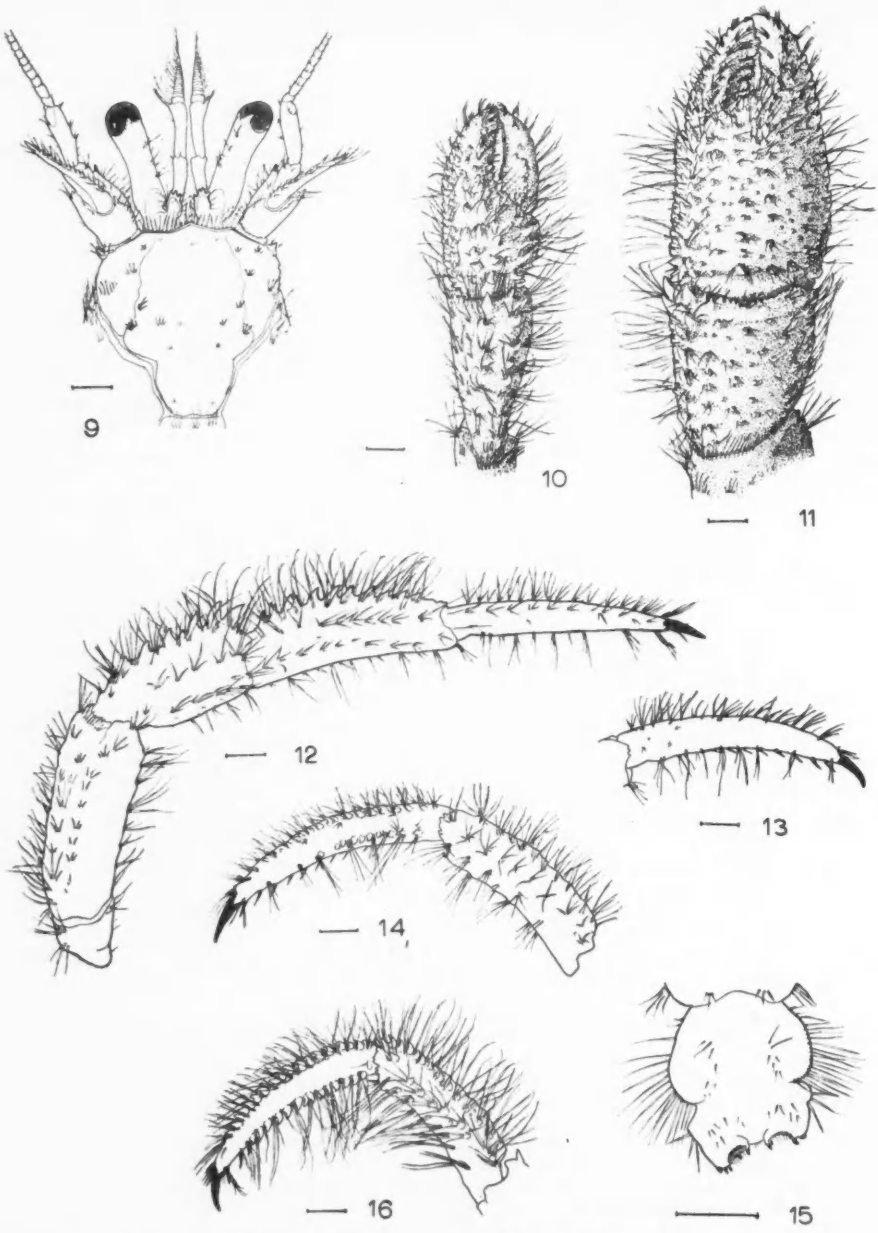


FIG. 8. *Pagurus quaylei* n.sp. Male.

Distal dorsal margins bordered with numerous small tubercles. A few tubercles on ventral distal margin. Chela longer than carpus but subequal in width. Inner margin of propodus straight and outer margin curved. Margins of fingers curved. Palm slightly convex dorsally: covered with tufts of long setae arising between numerous spiny tubercles of varying sizes. More tubercles on inner half and some in rows. Both fingers armed with median and lateral rows of small sharp tubercles. Gape between fingers, with teeth meshing only at distal third. Cutting teeth on fixed finger smaller than those of dactylus and tips of both corneus.

Left cheliped narrow, elongate, and setose. Ischium with a ventral longitudinal ridge armed with small teeth. Merus laterally compressed and narrower dorsally. Few scattered tubercles ventrally. Carpus subequal in length to merus. Many tufts of long setae, especially on inner face. Narrow dorsally, with 2 rows of large spiny tubercles. Chela slightly wider than carpus and somewhat less setose. 2 or 3 rows of spiny tubercles medially, ending between bases of fingers. Smaller spiny tubercles on either side of palm and a crowded semi-double row on each finger dorsally. Fingers elongated; gaping, except at tips. Fixed finger may have small



FIGURES 9–16. *Pagurus quaylei* n.sp. Male.

Fig. 9. Shield and head appendages; Fig. 10. Left chela and carpus; Fig. 11. Right chela and carpus; Fig. 12. Right second pereiopod; Fig. 13. Dactylus of right second pereiopod to show spines; Fig. 14. Propodus and dactylus of left third pereiopod; Fig. 15. Telson; Fig. 16. Propodus and dactylus of left third pereiopod of specimen from Santa Cruz Island, California.

TABLE 2. *Pagurus quaylei* n.sp. material examined.

Locality	Depth (*m*)	Bottom	Date	Station	Sex ♂	Sex ♀	Sex ♀♀	Collector
			British Columbia					
Qlawszeet, Stephens Is. 54°13′N, 130°45′W	Subtidal	Gravel	6/6/69		1			JFLH
Frederick Is. 53°56′N, 133°08.5′W	11	Sand & boulders	19/6/62	FRB 62-34	3			DBQ
Port Louis 53°42′N, 132°58′W	Subtidal	Gravel	4/6/69		12		10	JFLH
Checleset Bay 50°03′N, 127°39.8′W	34	Mud & sand	29/6/70	FRB 70-56	1		2	JFLH
Off Kyuquot 49°56.2′N, 127°24′W	34	Firm clean sand	29/6/70	FRB 70-64	1	1	1	JFLH
Nuchatlitz Inlet 49°45.7′N, 126°59′W	14	Firm clean sand	30/6/70	FRB 70-68		1	2	JFLH
Nasparti Inlet 49°45′N, 126°51′W	Subtidal		29/6/70		7	1	2	JFLH
Sydney Inlet 49°21.05′N, 126°14.7′W	13	Firm clean sand	30/6/70	FRB 70-70	4		3	JFLH
			California					
Entr. Albion River Est., Albion Bay, Mendocina Co.	Dredged		14/7/49	EB-43	1			
Outer Bodego Bay, adj. Doran Spit, Sonoma Co.	7–9		26/7/49	M63-49	13	6	21	L. O. Miles & W. K. Emerson
Outer Bodego Bay	5–9		3/8/49	M68-49	6	1		L. O. Miles & W. K. Emerson
San Luis Obispo Bay, San Luis Obispo Co.	15–26		4/8/38	V-3-885-38	2		3	
S San Miguel Is.	9–27		10/8/38	894-38	4		2	
Becher's Bay, Santa Rosa Is.	18		2/8/38	881-38	1			
N Santa Cruz Is.	97		14/9/38	898-38	1			
W Dutch Harbor, San Nicolas Is.	15–17		23/11/40	1204-40	4			
2¾ miles off Port Loma, San Diego Co.	17–24		23/2/41	1243-41	1			
			Mexico					
Inside Bahiá de San Quintín (San Quentin Bay), Baja California	4.5–8		14/4/51	V-4-2019-51	2	1		

separated teeth on inner margin and scattered tubercles on outer margin. Both fingers with a comb of short corneus setae on cutting surfaces.

Second right pereiopod slender and setose: longer than cheliped. Ischium short, setose. Merus compressed laterally, with dorsal and ventral surfaces narrow. Tufts of short setae. Carpus compressed laterally: inner face flat, outer convex. Dorsal ridge with large and small spiny tubercles. Propodus with inner face flat, outer convex. Dorsal ridge armed with smaller spiny tubercles than those on carpus. One spine on ventral distal margin. Dactylus slender, twisted at base and longer than propodus. Ventral spines small, claw long and curved.

Third right pereiopod. Ischium only slightly longer than that of second pereiopod. Merus with inner face

flattened, outer convex and dorsal and ventral surface with only ridges. Carpus like that of 2nd, but spiny tubercles smaller and fewer in number. Propodus with tufts of setae and a few flat granules. One spine on distal ventral margin. Dactylus longer than propodus and also than that of second pereiopod.

Left second pereiopod like right with smaller tubercles.

Left third pereiopod. Carpus with one distal spiny tubercle. Propodus with granules or spiny tubercles distally on outer face. Dactylus specialized: outer face with a row of spiny tubercles forming a ridge adjacent to dorsal crest. A similar ridge on lower part of same face. Much variation in degree of armament.

Telson with posterior lobes with lateral margins straight and corneus and armed with 2 or 3 large corneus spines distally. Posterior margin with concave spinulous edge and a large corneus spine on either side of cleft.

Colour of living animal — Shield dark red with a few brown spots and covered with a fine reticulation of pink with some yellow and orange medially. Light spots on dark brown of lateral part of carapace. Red at junction of shield and posterior carapace, which is pinkish-brown with poorly defined light blue stripes. Abdomen purplish-red with scattered yellow chromatophores. Tail fan orange and brown mottled. Antennule pale brown with scarlet chromatophores distally on second and third segments of peduncle: flagella translucent with orange at base of aesthetes. Antennal peduncle with first to third segments light brown, with red patches and some opaque white spots; fourth segment translucent mottled with dark brown. Flagellum translucent and banded with dark brown on certain segments: the pattern is irregular and made up of some all dark segments, others with two patches of dark brown on either side and the remainder without colour. Opaque white dots on clear segments, which occur every third or fourth segment. These disappear upon death. Eyestalk pale brown with red-brown and white chromatophores in interrupted stripes. Cornea black with brilliant silver chromatophores covering the surface except for 2 circular bands that curve over the distal part. Third maxillipeds greenish-brown with opaque white patches on distal part of each segment.

Right cheliped: ischium with patches of brown, merus dark brown or mahogany with spots of lighter colour and a white or pale brown band distally, carpus mottled grey or greenish-brown with pale grey spots and tubercles, hand with grey and white tubercles surrounded by reticulated greenish-brown to base of fingers, which are white except for a small brown streak medially on base of fixed finger. Left cheliped similar except that distal part of carpus is white and a tinge of grey-blue on distal part of palm. Walking legs: ischium with a few patches of brown, merus with band of red-brown, distal part of opaque grey-white, with a narrow band of mahogany and a wider band of pale yellow. Carpus grey-white and cream with 3 distinct dark red-brown stripes on outer surface, but none on inner surface. Propodus with 3 rows of grey spots separating four stripes of dark brown on the outer surface and 1 medial stripe on inner surface, none of which reach past the middle or last quarter of the segment, which is white with a yellow tinge distally. Dactylus with a dark grey patch proximally on a cream base, with 1 red-brown stripe dorsally on proximal half, and 1 red stripe on each lateral face medially, which reach almost to the brown claw. Fourth and fifth pereiopods red-brown with yellow rasps.

There is a tendency in preserved animals for the browns to become pink or red and the stripes less distinct.

Size — Shield length: males 1.0–4.3 mm, ovigerous females 1. 1–3.7 mm.

Range — Qlawdzeet, Stephens Island, B.C., 54°13′N, 130°45′W to Bahía de San Quintín (San Quentin Bay), Baja California, Velero IV stn. 2014–51. 2–97 m.

Habitat — Shallow water in gravelled areas.

Field characters — The banded flagella, dark stripes and white bands on carpi, propodi and dactyli of walking legs.

Notes — Ovigerous females were taken in British Columbia from June 4 to August 20, and in California from July 26 to August 10. Specimens from the group of islands off shore from Santa Barbara, California, are much more setose and more heavily armed with spiny tubercles and teeth but otherwise are similar morphologically.

The number of teeth on the eyescales varies from 1 to 5, and in any combination in any one individual. Over half of the specimens examined, of both sexes and all sizes, have 2 teeth on each scale. Of the remainder one or both scales had only 1 tooth in specimens of less than 2 mm shield length. 3, 4, or 5 teeth on the scales occurred in those of 1.5 mm to the largest of 4.3 mm shield length. A number of individuals have been kept alive in the laboratory and in some of these the number of teeth has increased. It would seem to require about three moults for the additional tooth to become subequal in size to the others. The extra teeth are apparently only produced on the inner margins.

Males kept in the laboratory for nearly 2 years have increased the length of the shield less than 0.1 mm per ecdysis, which occurred at intervals of 8–10 weeks. Growth of females was at an even slower rate, due possibly to the effects of egg production.

This is a very active hermit crab. It inhabits relatively small shells, which it can raise off the bottom and so move quickly over the surface and scale small rocks with ease. As this species seems to prefer subtidal gravelly areas, this agility would be of an advantage in such a habitat.

The rather striking modifications of the propodus and dactylus of the left third pereiopod of *P. quaylei* is not unique among the hermit crabs of the northeastern Pacific area. There is variation in the degree of modification in both individuals as well as in different species. Many *P. beringanus* (Benedict) have similar spiny tubercles on the propodus and dactylus, as do *P. hemphilli* (Benedict), *P. hirsutiusculus* (Dana), and *P. samuelis* (Stimpson). In these species the occurrence is less common than in *P. quaylei* and the tubercles are often fewer in number and less pointed. The advantages of this rather specialized modification of the pereiopod is not obvious. As all of these species are unusually active and inhabit rocky area, either in the surf zone or in the upper subtidal area, they are thus subjected to considerable buffeting, which could cause the animals to lose their grip on the substrate and to be turned upside down. The speed with which they are able to right themselves and to again cling is therefore of importance to their existence. The tip of the left third pereiopod would seem to be a crucial part of this process and thus the surfaces roughened by extra spiny tubercles might facilitate the speed or efficiency of the action.

This species is named for Daniel B. Quayle, whose knowledge of the marine invertebrates and their distribution in the northeastern Pacific is outstanding.

Pagurus stevensae n.sp.

Fig. 17–22

Pagurus brandti Stevens 1925 p. 285–286 fig. 7. Hart 1940 p. 93. Bakus 1966 p. 427.

Material examined — Table 3.

Description — Carapace shield subequal in length and width in small specimens but slightly longer than wide in large. Smooth surface with tufts of short setae. Rostrum obtuse, rarely pointed, and little advanced beyond broad lateral teeth, each of which has a small curved submarginal tooth. Soft plumose setae on lateral carapace.

Eyestalk long and slender, slightly constricted medially, and more than half width of shield. Cornea slightly wider than base of stalk. Scales somewhat triangular with large submarginal tooth.

Antennular peduncle reaching beyond eyes.

Antenna with minute lateral tooth on basal segment of peduncle. Second segment with 1 tooth on inner distal point, 1 at base of acicle and 1 short stout outer process with 2–7 teeth distally. Setose acicle curved, decreasing in width distally, and terminating in a sharp pointed tip, which barely reaches cornea in small individuals but may surpass it in large. Third segment of peduncle short, and fourth flattened and slender. Peduncles of antennule and antenna subequal in length. Flagellum may be longer than right cheliped.

Third maxilliped with 3–4 teeth on inner margin of basis. Ischium with a series of small corneus teeth, crista dentata, plus 1 accessory tooth medially. Merus with 0–2 spiny tubercles on ventral surface.

Right cheliped elongate and narrow dorsally. Ischium with spiny tubercles scattered on inner ventral margin. Merus with spiny tubercles on ventral lateral margins and a few medially. Lateral face slightly convex and inner face setose. Distal dorsal surface with flat setose ridges and margin cut into 3–7 teeth. Carpus subequal or longer than merus, bulbous ventrally and lateral faces flat. Inner dorsal margin with several rows of stout corneus-tipped tubercles. A concentration of small tubercles on outer margin but not placed in clearly defined rows. Width of distal carpus equal to less than half length in large individuals but often half or slightly more in small. Distal dorsal margin armed with spiny tubercles. Chela with outer margin of palm curved and inner almost straight. A broad ridge covered with many spiny tubercles on inner dorsal surface. An inverted elongated V-shaped raised area delineated with spiny tubercles on mid-dorsal palm and separated from inner ridge by a sparsely tuberculated groove. Outer slightly convex side with numerous small spiny tubercles and tufts of short setae. Outer margin of chela outlined with a row of large spiny tubercles, with corneus tips sharp and upturned, especially on fixed finger. Fingers flat, with scattered tubercles on fixed finger and rows of closely set spiny tubercles on dactyl. Cutting surfaces with broad flat teeth.

Left cheliped ischium with serrated ventral ridge. Merus with ventral margins armed with large spiny tubercles, dorsal surface narrow and armed with setose ridges. 1–2 teeth on distal dorsal margin. Carpus with scattered spiny granules and fine setae on ventral and outer faces; somewhat swollen distally. Mid-dorsal area narrow and bordered on either side with a row of spiny tubercles; inner face setose. Chela with outer margin curved and outer face oblique and slightly convex: covered with many small spiny tubercles and granules. A median crest with 2 rows of spiny corneus-tipped tubercles (inner row larger); tubercles alternate and point in opposite directions and decrease in size distally disappearing at middle of fixed finger. Inner face smooth, with groove adjacent to crest and inner margin with 1 or 2 rows of small spiny tubercles. Dactylus with scattered granules. Fingers with cutting surface armed with short stout corneus setae and tips corneus.

Walking legs long and slender, laterally compressed, dorsally setose with tufts of short setae. Right second pereiopod with short ischium. Merus with ventral margin serrate. Carpus short with a dorsal crest of spiny tubercles. Propodus slightly shorter than dactylus, with small spines on ventral margin. Dactylus with a row of long spines ventrally and dorsally a double row of small spines, which are more obvious in large individuals. Left second pereiopod similar to right. Third pereiopod with ischium longer than that of second, but whole limb subequal in length. Only 1 tooth or none on

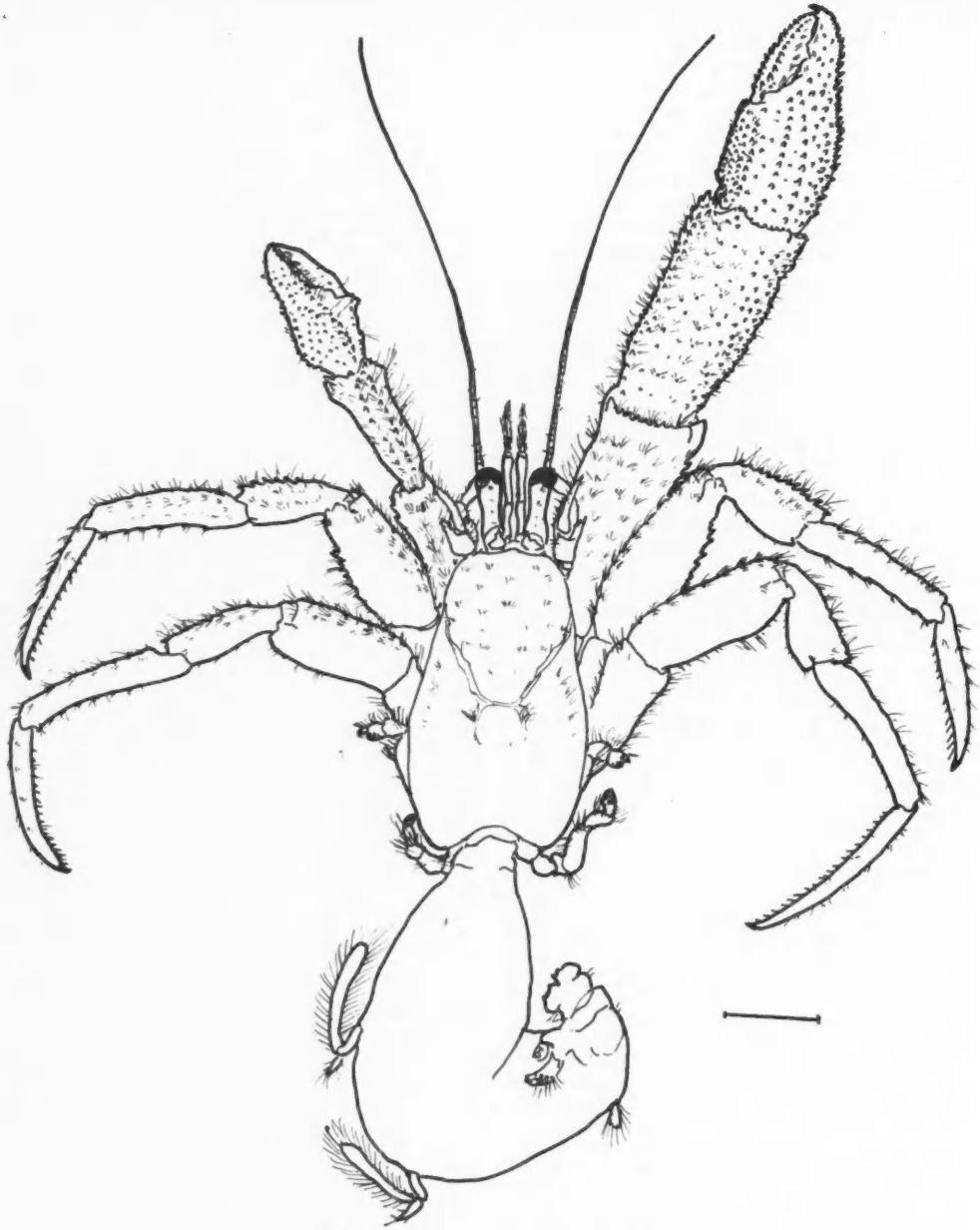
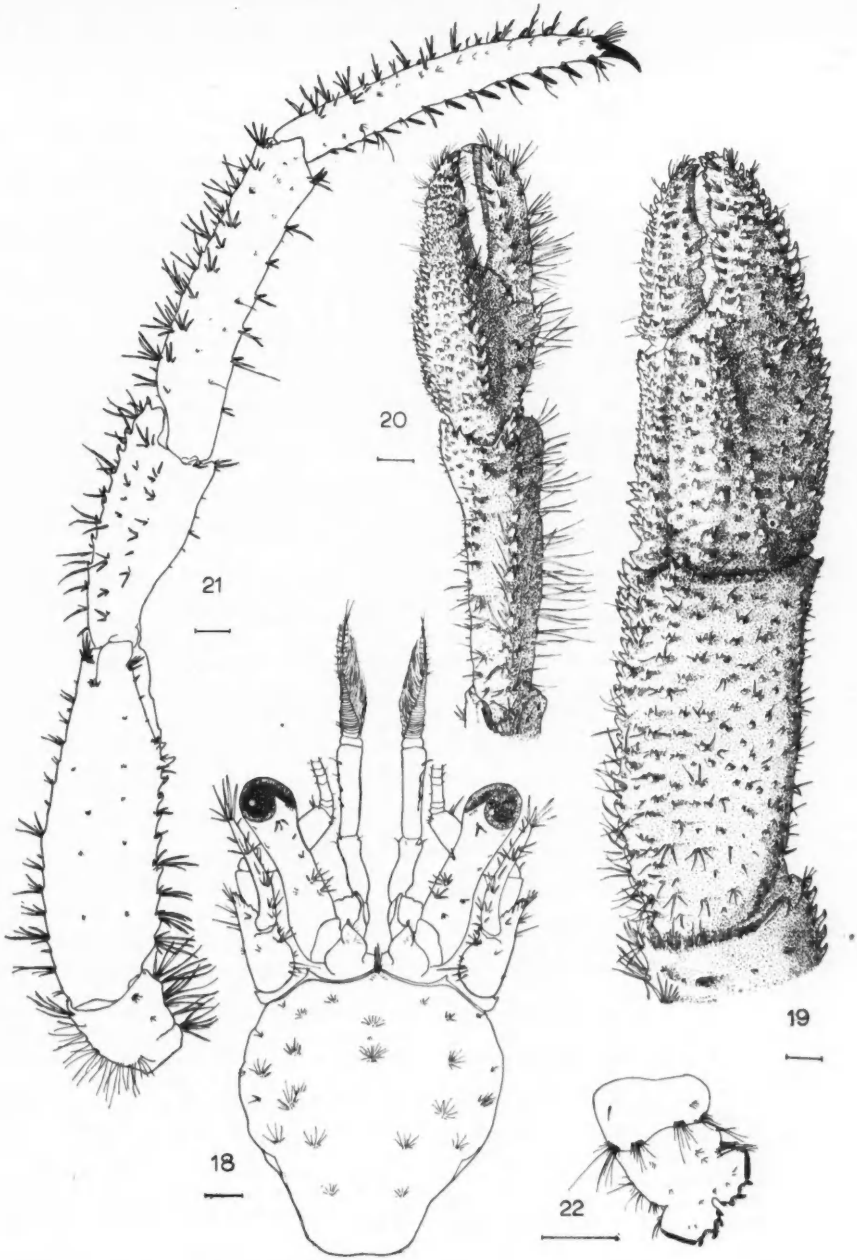


FIG. 17. *Pagurus stevensae* n.sp. Male.



FIGURES 18–22. *Pagurus stevensae* n.sp. Male.
Fig. 18. Shield and head appendages. Fig. 19. Right chela and carpus; Fig. 20. Left chela and carpus; Fig. 21. Right second pereiopod. Fig. 22. Telson.

TABLE 3. *Pagurus stevensae* n.sp. material examined.

Locality	Depth (*m*)	Bottom	Date	Station	Sex ♂	Sex ♀	Sex ♀♀	Collector
Off Langara Is.	36	Sand	5/6/69	FRB 69-7	23	34	1	JFLH
54°12.9′N, 132°57.3′W								
" " "	118	Mud & sand	5/6/69	FRB 69-9	23	21		JFLH
54°12.55′N, 132°53.6′W								
" " "	54	Mud & sand	5/6/69	FRB 69-8	8	19		JFLH
54°12′N, 132°54.5′W								
Dixon Entrance	150	Sand	28/5/65	FRB 65-9	2			DBQ
54°11′N, 131°50.1′W								
Hecate Strait	85	Sand & boulders	6/6/69	FRB 69-10	3			JFLH
54°11′N, 131°0.8′W								
Wright Is, Petrel Chn.	66	Gravel	3/6/65	FRB 65-27	1			DBQ
53°44′N, 130°30′W								
North tip Anger Is.	70	Mud	3/6/65	FRB 65-25	1			DBQ
53°42′N, 130°31′W								
Hecate Strait	55	Rock & clay	6/8/65	FRB 65-49	7			DBQ
53°32′N, 131°09′W								
Off Goose Is.	106	Sand & gravel	8/69	FRB 69-34	2			DBQ
51°51.4′N, 128°31′W								
Queen Charlotte Sd.	108	Rocks & gravel	26/6/70	FRB 70-29	1			JFLH
51°14′N, 128°36.5′W								
" " "	119	Boulders	8/68	FRB 68-8	1			DBQ
51°09′N, 127°55.5′W								
" " "	52	Gravel & sand	25/6/70	FRB 70-25	1			JFLH
51°07.3′N, 127°41.3′W								
" " "	48	Sandy mud & gravel	25/6/70	FRB 70-26	5	5		JFLH
51°07.3′N, 127°41.3′W								
Seymour Inlet	45	Sand & gravel	25/6/70	FRB 70-24	1	1		JFLH
51°05′N, 127°39′W								
Queen Charlotte Sd.	98	Mud & clay	26/6/70	FRB 70-35	1	3		JFLH
50°59.2′N, 129°19.5′W								
Seymour Inlet	112	Mud & gravel	24/6/70	FRB 70-22		1		JFLH
Off Scott Is.	198	Boulders & rock	10/9/64	FRB 64-205	1	1		DBQ
50°40′N, 128°48.5′W								
Malcolm Is.	60	Shell & gravel	12/1/63	FRB 63-3	1		1	DBQ
50°37.7′N, 127°03.8′W								
Off San Josef Bay, V.I.	75	Mud & sand	8/67	FRB 67-65	2			DBQ
50°34.5′N, 128°22.2′W								
Off Quatsino Sd.	38	Gravel	29/5/69	FRB 69-4	3	3		JFLH
50°30.4′N, 127°43.1′W								
Checleset Bay	20	Sandy mud	29/6/70	FRB 70-54		1		JFLH
50°10.4′N, 127°37.5′W								
Checleset Bay	44	Coarse gravel	29/6/70	FRB 70-53	31	71		JFLH
50°0.2′N, 127°45.5′W								
Off Kyuquot Sd.	26	Clean gravel	29/6/70	FRB 70-63	1			JFLH
49°48.9′N, 127°30.6′W								
Off Brooks Peninsula	42	Fine clean gravel	28/6/70	FRB 70-49	1			JFLH
49°20.5′N, 128°09′W								
Off McKay Pt. Newcastle Is.	64		6/8/34		1			JFLH
49°13′N, 123°52′W								
Entr. Departure Bay	73	Rocks & glass sponge	1/6/33		1			JFLH
49°13′N, 123°52′W								
Satellite Chn.	72	Mud	16/10/65		1			JFLH
48°44′N, 123°25′W								
Off Cape Flattery	114	Gravel	9/68	FRB 68-43	1			DBQ
48°16.0′N, 125°24′W								

distal ventral part of merus. Carpus with small spiny tubercle on upper distal tip, with or without small tubercles on mid-dorsal ridge. Ventral spines on propodus, minute. Dactylus similar to that of second but with 2 extra rows of small spines on anterior face. Dactylus longer than propodus.

Telson with posterior lateral lobes large and usually wider than anterior lobes. The protuberant proximal part of posterior lobe subrectangular, with lateral posterior margin a narrow corneus plate, and posterior curved margin bearing 4 large curved corneus spines: the outer separated from the 3 equidistant inner by a greater hiatus. Median cleft short and narrow.

Colour of living animal — Shield white with red and tan reticulations; lateral areas yellow and posterior part of carapace and abdomen like shield. Some red spots scattered over surface. Tail-fan white with tan mottling. Segments of peduncle of antennule with median scarlet bands, flagella with orange base to aesthetes. Peduncle of antenna pale orange with red patches and flagellum reddish translucent. Eyestalk pale orange with red interrupted stripes, cornea with green and yellow surface chromatophores. Maxilliped red with white bands at junctions of segments.

Chelipeds pinkish-brown with dark red spiny tubercles and with scattered small red spots, fingers pale pink. Walking legs with ischium white with red reticulations, merus similar but with two lighter patches medially, carpus dark red-brown with lighter patches mediolaterally, propodus with a dark red stripe dorsally and one ventrally and an orange stripe midlaterally on light yellow base, dactyl with a red-brown band proximally and thin red or orange stripes, dorsally, ventrally, and midlaterally on light base with interrupted rows of red spots above median stripe.

Small individuals are usually more brilliant in colouring than large, scarlet and orange being replaced in large specimens by an overall tan. In preserved material the colour is more drab, although the small red spots seem to persist.

Size — Length of shield: males 1.0–11 mm, and females 1.6–9 mm (ovigerous females 2.2–9 mm).

Range — Dixon Entrance, B.C., 54°12.9′N, 132°-57.3′W, to San Juan Archipelago, Puget Sound, Washington (Stevens 1925). 13–198 m.

Habitat — On mud, sand, or gravel bottom. Often occupy living sponges, *Suberites ficus* (Johnston). These sponges are usually tan, and often have red, orange, or pink blotches. The original shell would appear to be absorbed by the sponge but the cavity is retained and increased as necessary with the growth of the crab.

Field characters — In large specimens, the right cheliped, with its elongate carpus and no distinct white band on the distal merus, plus the scattered small red spots and the dactyli of the walking legs with a row of small red spots above the dark stripe, serve to distinguish this species from *P. dalli* (Benedict). The brilliant colour of small individuals and the dactyl spots are distinctive.

Notes — Ovigerous females have been taken in January off Malcolm Island and in June in Dixon Entrance.

There are at least four allied species of *Pagurus* found in the northeastern Pacific and in the Arctic, whose validity as distinct species has been the subject of considerable controversy. To date, only two of these have been found in British Columbia: *P. dalli* (Benedict) and *P. stevensae*. The latter has been recorded as *P. brandti* by Stevens (1925), Hart (1940), Bakus (1966), and synonomized by Makarov (1938) as *P. pubescens* Kröyer. I have examined specimens of *P. pubescens* from the Canadian Eastern Arctic and a syntype of Benedict's *P. brandti*. Both *P. dalli* and *P. stevensae* differ from these two species in a number of features, but the most easily diagnosed difference is in the size and shape of the eyes and eyestalks. In the latter two species the eyestalk is elongate, equal to or more than one-half the width of the shield, and the cornea is little, if any, wider than the diameter of the stalk. The eyestalks of *P. brandti* and *P. pubescens* are short, equal to one-half or less than the width of the shield, and the diameter of the cornea is much greater than the diameter of the eyestalk. The proportionate size and shape of the eyes and eyestalks would seem to be a consistent character for both large and small individuals.

Pagurus stevensae can be distinguished from *P. dalli* by the shape and armature of the carpus of the major cheliped. The dorsal surface of the carpus of *P. stevensae* is elongate: in large individuals twice as long as wide, with subparallel margins, the outer one of which is roughly marked with small tubercles. The carpus of *P. dalli* is not particularly elongate, increases in width distally, and the outer margin is clearly marked by a distinct row of large spiny tubercles. The telson of *P. stevensae* has the distal lobes wider than the proximal and the margins are angled, whereas the lobes of the telson of *P. dalli* are subequal in width and the margins of the distal ones are rounded. The living animals differ in colour: *P. stevensae* is an overall pinkish brown, red, or orange with scattered small red spots, which are characteristically in a row on the upper half of the dactyls of the second and third pereiopods, whereas *P. dalli* is an overall brown with opaque white bands on the distal part of the meri of the first three pairs of pereiopods.

This species is named for the late Belle A. Stevens, of Seattle, Washington, whose enthusiasm for the

taxonomy of the decapod Crustacea of the Puget Sound area inspired all of us who knew her.

New Records and Extensions of Range of Species in the Area Between 48° and 55°N and 123° and 135°W

Calastacus quinqueseriatus Rathbun 1902

FRB stn 64-213, west of Queen Charlotte Sound, 50°54.5′N, 130°06′W, Sept. 11, 1964, 2200 m, mud, 1 female, damaged. DBQ.

The collection of this specimen is a northern and eastern extension of known localities, as well as from a greater depth. The previous northern record of the eastern Pacific is off Point Sur, California (36°20′N) from 1220 m, and the southern off San Nicholas Is., California, 293–2013 m (Schmitt 1921). The nearest western record is from the Okhotsk Sea, 288–1150 m (Vinogradov 1947).

Callianassa gigas Dana 1851

Wainwright Basin, 54°15′N, 130°20′W, Aug. 4, 1967, 2 males (immature). M. Waldichuk. Inside Sandspit Bar, Line #3, 26 m, Sept. 14, 1960, 1 dried specimen. DBQ.

The paucity of specimens of this species collected in British Columbia is probably due to the difficulties of collection from burrows in sticky mud of the lower intertidal or subtidal. Wainwright Basin, near Prince Rupert, is much farther north than Boundary Bay. The southern known limit is San Quentin Bay, Lower California (Stevens 1928). This species has been taken from 26 m as reported above and from 48–51 m dredged from northeast of Orcas Island, Puget Sound, Washington, 48°42.8′N, 122°49′W, July 24, 1964, by P. L. Illg.

Paguristes turgidus (Stimpson 1857)

FRB stn. 71-66, Dixon Entrance, 54°36.0′N, 132°-08.0′W, 157 m. Sept. 22, 1971, 1 female. JFLH. This is a northern extension from Rennell Sound, Queen Charlotte Is. (Hart 1940). The recorded southern limit is San Diego, California (Schmitt 1921).

Paguristes ulreyi Schmitt 1921

Frederick Island, 53°56′N, 133°08.3′W, littoral, in rocky crevices, June 3, 1969, 6 males, 11 females. JFLH. The previously known northern record was Monterey, California, and the southern record by Haig et al. (1970) is the outer Baja California coast, and in Golfo de California as far north as Punta Gorda. To a depth of 56 m (Schmitt 1921).

Pagurus cavimanus (Miers 1879)

Entrance to Departure Bay, 49°10′N, 123°50′W, 73 m, June 1, 1933, 1 small male. JFLH. This record constitutes a considerable southerly extension of range from the previous record from Juneau, Alaska, 58°18′N, 134°25′W. 35–250 m (Rathbun 1904). The northern and western range is the Bering Sea and Japan (Miers 1879; Yokoya 1933). The collection by C. Birkeland, by scuba diving, from Cobb Seamount, north rim, 46°44′N, 130°47′W, 37 m, of a large male, is a fascinating record (Birkeland 1971).

Pagurus cornutus (Benedict 1892).

FRB st. 68-45, west of Barkley Sound, 48°44.5′N, 126°30.3′W, 436 m, rock, Sept. 1968, 2 males, 5 females. DBQ. The previously known southern record was off Queen Charlotte Sound, B.C. (Rathbun 1904). The northern and western known limits are the Bering Sea and the Commander Islands. 160–830 m. (Makarov 1938).

Pagurus hemphilli (Benedict)

Lucy Island, off Langara Island, 54°10′N, 132°58′W, littoral, June 5, 1969, 6 males, 2 females. JFLH. This is farther north than the previous record of Houston Stewart Channel (Hart 1940). The southern known limit is Monterey, California (Schmitt 1921).

Pagurus samuelis (Stimpson 1857)

Louie Bay, south side of Nuchatlitz Inlet, Nootka Sound, 49°45′N, 126°50′W, high intertidal, May 28, 1969, 27 males, 29 females (22 ovigerous). JFLH. The occurrence of this species on the west coast of Vancouver Island extends the known range farther north than has been recorded in the literature, with the exception of Rathbun's (1904) report from Sitka, Alaska. However, Schmitt (1921) states that this record was based on a misidentification of *P. hirsutiusculus* (Dana). The known southern limit is Northwest Baja California (Haig et al. 1970). *P. samuelis* is recorded from Japan, but Holmes (1900) questioned this record. I have examined specimens from Japan, identified as this species, but which differ from those found in California, and in British Columbia, both in colour and in form.

Orthopagurus minimus (Holmes 1900)

FRB stn. 62-34, Frederick Island, 53°56′N, 133°-08.7′W, 11 m, sand and boulders, Aug. 1962, 1 female (ovigerous). DBQ. This locality is north of Skidegate, Queen Charlotte Islands (Hart 1940). The southern known limit is San Diego, California, 27–64 m (Schmitt 1921). The western record is Nel'ma Bay, Tartar Strait (Makarov 1938). 11 m is a shallower habitat than previously recorded.

Parapagurus pilosimanus Smith 1879

FRB stn. 71-45, off Queen Charlotte Islands, 53°02.0′ N, 132°51.8′W, 1204 m, mud, Sept. 18, 1971, 1 male, 4 females (ovigerous). JFLH. FRB stn. 64-197, off Vancouver Island, 49°19′N, 127°25.6′W, 1400 m, mud, Sept. 6, 1964, 5 males and 2 females. DBQ. The distribution of this species is world wide in deep water. According to Makarov (1938) it occurs between 210 and 4000 m and to 53°N. In the North Pacific it has been taken from near Kamchatka (52°-42.5′N, 159°03.5′E) (Makarov 1938) but apparently has not been previously recorded from the northeastern Pacific.

Petrolisthes cinctipes (Randall 1839)

Port Louis, Queen Charlotte Islands, 53°42′N, 132°-58′W, littoral, between *Mytilus californianus* Conrad on exposed rocks, June 4, 1969. 3 males, 3 females (ovigerous). JFLH. This collection is farther north than the former record of Rose Harbour, Houston Stewart Channel (Hart 1940). The southern known limit is Santa Barbara and offshore Islands. To 54 m (Haig 1960).

Munidopsis quadrata Faxon 1893

FRB stn. 71-44, off Queen Charlotte Islands, 53°01.5′N, 132°54.3′W, 1069 m, mud and gravel, Sept. 18, 1971, 1 male, 2 females (1 ovigerous, eggs large). JFLH. This species has been previously recorded off Destruction Island, Washington, and south to Tres Marias Islands, Mexico, from 86 to 1572 m (Rathbun 1904).

Chionoecetes tanneri Rathbun 1893

FRB stn. 65-66, west of Englefield Bay, Queen Charlotte Islands, 53°01′N, 132°55′W, 1190 m, mud, Aug. 10, 1965. 14 juveniles. DBQ. The previous northern limit recorded in the literature is Washington, 47°29.3′W and the southern Lower California, 37°17′N, from 50 to 1940 m (Rathbun 1925).

Scleroplax granulata Rathbun 1893

Roller Bay, 50°55′N, 127°57′W, littoral, July 22, 1959, 1 juvenile. DBQ. This record from the northern tip of Vancouver Island extends the northern limit of known range from Esperanzo Inlet (Hart 1940). The southern known limit is Ensenada, Lower California (Rathbun 1918).

Pinnotheres pugettensis Holmes 1900

Spider Anchorage, 51°45′N, 128°05′W, scuba 6 m, Aug. 22, 1969, 1 female from purple-hinged scallop (*Hinnites giganteus* Gray). F. R. Bernard. The collection of this pinnotherid from northern Vancouver Island is an extension of range from the previous northern record of Departure Bay, Vancouver Island (Taylor 1912). The southern limit is Puget Sound (Holmes 1900). Taylor (1912) reported a specimen from *Mya arenaria* Linnaeus but Rathbun (1918) reports tunicates as the only host. *Hinnites* is thus an unrecorded host.

Pinnotheres taylori Rathbun 1918

Cape Lazo, 49°40′N, 124°50′W, Feb. 5, 1969, 2 females in *Ascidia paratropa* (Huntsman). THB. FRB 69-4, Quatsino Sound, 50°30.4′N, 127°43.1W, 38 m, May 29, 1969, 1 female in *Phallusia ceratodes* Huntsman, JFLH. Until recently this species was known only from Departure Bay and Ucluelet, B.C. (Rathbun 1918). It has been recorded from Puget Sound by Pearce (1966) and Lie (1968). The above records extend the known range some distance north on both the east and the west coasts of Vancouver Island.

Planes marinus Rathbun 1914

20 miles west of Ucluelet, Vancouver Island, 48°57′N, 125°35′W, May 1963, 2 females from a net-covered Japanese glass float. I. MacAskie. This record is slightly farther north than that reported south of Vancouver Island (Hart 1959). This species has been found from the coast of Oregon, off Baja California, Mexico, Hawaii, New Zealand, and St. Helena Island, South Atlantic (Chace 1966).

SPECIES NOT PREVIOUSLY RECORDED FOR BRITISH COLUMBIA

Pagurus capillatus (Benedict 1892)

Common in shallow water (to 90 m) on muddy bottom, but apparently not previously reported from British Columbia. The distribution is the Arctic Ocean, southward through Bering Strait to Kamchatka and California. 5–439 m (Rathbun 1904). Schmitt (1921) gives the California record as off Santa Cruz, 439 m. Also reported from northern Korea and the Sea of Okhotsk (Makarov 1938).

Pagurus tanneri (Benedict 1892)

FRB stn. 68-52, West of Clayoquot Sound, 49°04.5′N, 126°51.5′W, 304 m, boulders, Sept. 1968, 1 male, 1 female. DBQ. FRB stn 76-1-41, La Perouse Bank, 48°45′N, 126°31′W, 580 m, 1967, 15 males, 6 females (3 ovigerous). S. J. Westrheim. There does not seem to be a record in the literature of this species collected in British Columbia. The known range is from Iliuluk Harbor, Unalaska, to off San Simeon Bay, California, 92–1053 m (Rathbun 1904).

Paralomis verrilli (Benedict 1894)

FRB stn. 68-29, southwest of Barkley Sound, 48°-13′N, 126°18.5′W, 951 m, mud and sand, Sept. 1968, 1 juvenile. DBQ. This species does not seem to have been recorded from this area. The range is from Okhotsk Sea, 450 m (Vinogradov 1947) to off Cortez Bank, California, 1238–1480 m (Rathbun 1904).

Lithodes couesi Benedict 1894

FBR stn. 71-65, Dixon Entrance, 54°32.0′N, 132°05.3′W, 258 m, rocks, Sept. 22, 1971, 1 juvenile. JFLH. FRB stn. 71-43, west of Englefield Bay, Queen Charlotte Islands, 53°00.8′N, 132°55.8′W, 1076 m. Sept. 18, 1971, 1 male. JFLH. This species apparently has not been recorded from this area, nor as deep nor as shallow as the specimens obtained in 1971. The range is from the Bering Sea to off San Diego, California, 550–970 m (Schmitt 1921).

Acknowledgments

The major part of the collections were made by staff members of the Fisheries Research Board of Canada, working from the Biological Station at Nanaimo, B.C. During certain periods between the years 1929 and 1940, during periods in the summers of 1969, 1970, and 1971, I made collections using facilities of this institution. Since 1940, my collecting activities have been off southern

Vancouver Island, including parts of the west coast exposed to the open Pacific.

Originally J. Haig, Allan Hancock Foundation, Los Angeles, California, planned to describe *Pagurus quaylei*, using specimens from California and Mexico, and P. A. McLaughlin, University of Miami, Florida, was to collaborate with me to describe *P. stevensae*. However, due to other commitments, neither have had time to do so; thus, they have kindly suggested that I describe these two forms.

I thank both of these colleagues for their confidence in me and for help and loan of material. I also acknowledge the consideration of staff members of the Biological Station at Nanaimo, who over the years kept my specimen requests in mind and succeeded in capturing so many hoped-for species. I am particularly grateful to D. B. Quayle, T. H. Butler, and F. R. Bernard for making so much reptant decapod material available for me to study. Last, but not least, I want to acknowledge the constant help and encouragement given to me by my late husband, G. C. Carl.

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Some Effects of Salinity and Temperautre on Early Development of Pacific Herring (*Clupea pallasi*)

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ALDERDICE, D. F., AND F. P. J. VELSEN. 1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Bd. Canada 28: 1545–1562.

Pacific herring (*Clupea pallasi*) eggs were incubated in the laboratory at 13 different salinity–temperature combinations (ranges: 5–45‰ S, 4–14 C). Data were obtained on rate of development, larval length at hatching, percent total hatch, and percent viable hatch. Subsamples of larvae, held in their incubation media, provided data on posthatching survival and larval size at yolk sac absorption. Maximum percent viable hatch, larval size at hatching, and maximum survival to yolk sac absorption occurred in a trial at 16.41‰ S, 6.85 C. Optimum conditions were calculated by response surface analysis — maximum total hatch: 12.01‰ S, 6.46 C; maximum viable hatch: 16.98‰ S, 8.33 C; maximum length of newly hatched larvae: 20.00‰ S, 5.54 C. Maximum percent viable hatch of largest larvae in the shortest incubation period is estimated to occur at or near 16.98‰ S, 8.7 C. Abnormalities of the lower jaw were present in larvae from eggs incubated at temperatures of 4.0 and 4.71 C. Pacific herring eggs are considered euryhaline and stenothermal. A comparison of laboratory and field observations suggests that occurrence and abundance of herring is related to the availability and extent of spawning salinities between 8 and 28‰. Moreover, catch statistics suggest that population abundance in North American waters is associated with spawning temperatures of 5–9 C, abundance is limited by temperatures of 9–10 C, and the maximum temperature for spawning is about 10 C. From the current study, survival of viable larvae to yolk sac absorption would place the lower limit of thermal tolerance of Pacific herring eggs between 4 and 5 C.

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Des oeufs de hareng du Pacifique (*Clupea pallasi*) furent soumis à l'incubation en laboratoire à différentes combinaisons de température et de salinité (gammes de 5–45‰ S et de 4–14 C). Nous avons noté les taux de développement, longueur des larves à l'éclosion, pourcentage d'éclosion totale et pourcentage d'éclosion viable. Des sous-échantillons de larves, conservées dans leur milieu d'incubation, nous ont permis de déterminer le pourcentage de survie après l'éclosion et la longueur des larves au stade de résorption du sac vitellin. Nous avons obtenu des valeurs maximales d'éclosion viable, de taille des larves à l'éclosion et de survie jusqu'à la résorption du sac vitellin au cours d'un essai à 16.41‰ S et 6.85 C. Le calcul des conditions optimales a abouti aux chiffres suivants: éclosion totale maximale: 12.01‰ S et 6.46 C; éclosion viable maximale: 16.98‰ S et 8.33 C; longueur maximale des larves à l'éclosion: 20.00‰ S et 5.54 C. Le plus fort pourcentage d'éclosion viable des larves les plus grandes après la période d'incubation la plus courte se situe à environ 16.98‰ S et 8.7 C. Nous avons observé des difformités à la mâchoire inférieure des larves provenant d'oeufs incubés à 4.0 et 4.71 C. Les oeufs de hareng du Pacifique sont donc euryhalins et sténothermiques. Ces observations en laboratoire comparées à celles faites en nature suggèrent que l'occurence et l'abondance du hareng sont fonction de la disponibilité et de l'étendue pour la ponte de salinités de 8–28‰. L'analyse des statistiques de capture suggère de plus que l'abondance des populations dans les eaux de l'Amérique du Nord est associée à des températures de 5–9 C au moment de la ponte. Des températures de 9–10 C en limitent l'abondance, alors que la température maximale pour la ponte est d'environ 10 C. D'après le pourcentage des larves qui atteignent le stade de résorption du sac vitallin, tel qu'observé au cours de la présente étude, la limite inférieure de tolérance thermique des oeufs de hareng du Pacifique se situe entre 4 et 5 C.

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HISTORICALLY, the Pacific herring (*Clupea pallasi*) is said to occur around the rim of the North Pacific Ocean from San Diego, California (32°45′N, 117°10′W) to Toyama Bay, Honshu (37°N, 145°E), and the shores of Korea bordering the Yellow Sea (Svetovidov 1952). However, in recent years, the southern limits of commercial catch appear to have retreated somewhat northward. Herring stopped visiting Honshu spawning grounds in numbers in the early 1900's (Kasahara 1961; Motoda and Hirano 1961). In recent years catches of herring — although never large — have been incidental, on the average, south of Monterey, California (36°45′N, 122°W). Northward in North American waters Pacific herring are recorded as far as Port Clarence, Alaska (65°15′N, 166°40′W), and in Asian waters as far as Olenek Bay (Laptev Sea, Arctic Ocean, 73°15′N, 147°E). In the Canadian literature the Pacific herring generally is given specific rank, whereas Russian workers consider it a subspecies (*C. harengus pallasi*) of the Atlantic herring (Svetovidov 1952).

In British Columbia waters spawning usually takes place from February to early May, within or just below the intertidal zone (Stevenson 1962; Taylor 1964, 1971) where considerable variations in salinity and temperature can occur. Spawning usually occurs in protected waters, the eggs being attached to submerged aquatic vegetation, usually eelgrass (*Zostera* and *Phyllospadix*), *Sargassum*, or *Fucus* (Taylor 1964). Many other types of vegetation, as well as bare rock, may be utilized; in California, dense beds of eelgrass may be avoided in favour of what would appear to be less suitable substrate (Miller and Schmidtke 1956).

Although attention in the present instance is directed to salinity and temperature tolerance of eggs and larvae, other potential causes of egg mortality include wave action, exposure to the air and predation by birds (Taylor 1964). In a laboratory study, Taylor (1971) found substantial increases in egg mortality in samples simulating high densities of egg deposition, presumably resulting from respiratory difficulties in closely packed eggs (see also Blaxter 1956; Galkina 1968). Larvae are also subject to predation by ctenophores, jellyfishes, and chaetognaths (Stevenson 1962; Fraser 1969).

Available evidence suggests that eggs and larvae from both North American and Asian waters can tolerate a broad range of salinities (Svetovidov 1952; McMynn and Hoar 1953; Kurata 1959; Stevenson 1962) and, in this respect, they resemble similar stages of the Atlantic herring (*Clupea harengus*) (Holliday and Blaxter 1960; Blaxter and Holliday 1963). Effects of temperature on egg development have been reported by McMynn and Hoar (1953), Outram (1955), and Taylor (1971) for eggs from British Columbia waters, and have been summarized for Asian studies by Svetovidov (1952) and Motoda and Hirano (1961).

The current laboratory experiments were undertaken to provide evidence on the tolerance of incubating eggs and early larvae of Pacific herring to salinity and temperature acting in unison. Laboratory data on tolerance are compiled, compared with field observations of levels of salinity and temperature in spawning areas, and some general associations are indicated.

Materials and Methods

Adult herring were taken at Ganges Harbour, B.C. (48°50′N, 123°27′W) by the vessel *A. P. Knight* on March 10, 1970. The live fish were transported to the Biological Station and held until the following day. Eggs were expressed on to small rectangles of nylon mesh (7.5 × 3.5 cm, 9 filaments/cm) to form on each rectangle a continuous strand of eggs one layer thick. Eggs were fertilized in sea water (28.42‰ S) at 9 C. Average egg diameter (N = 40) 2.7 hr after fertilization was 1.57 ± 0.05 mm in 28.55‰ S. The prepared mesh swatches were curled into incubator cells (Alderdice and Velsen 1968). Incubators were held in 40-litre tanks at constant salinity–temperature conditions. Egg samples in each incubator were perfused at a water velocity of 260 cm/hr for the first 2 days after fertilization, and at 500 cm/hr thereafter. The developing eggs were exposed to normal laboratory lighting for a 10-hr period daily, beginning at about 7:00 AM.

Thirteen salinity–temperature combinations were employed in 14 experimental trials (Table 1). To the nine trials of a 3^2 factorial design (or $2^k + 2(k) + 1$ composite design with $k = 2$) were added four internal points ± 0.5, ± 0.5 units from the centre (0, 0). To achieve orthogonality the axial points of the design (0, $\pm\alpha$; $\pm\alpha$, 0) were spaced $\alpha = 1.1648$ units from the replicated centre. The design provided reasonably uniform coverage of the salinity–temperature test space at seven different levels of the two variables. Four subsamples of eggs were incubated in each of the 14 trials. The number of eggs per subsample (Table 1) averaged 453 (range 299–726).

Egg development was monitored daily by gross inspection of each incubator until 1 or 2 days prior to the time of expected hatching. Incubator cells were then opened at 8-hr intervals, at which time all newly hatched larvae were removed, until hatching was complete. At each of these intervals, samples of 10–25 anaesthetized larvae, numbers permitting, were measured by ocular micrometer for total length (including caudal fin fold) and antero-posterior yolk sac length, until a majority of eggs had hatched in each incubator. Measurements were confined to viable larvae, those considered normal in physical appearance.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

TABLE 1. Salinity–temperature combinations of the design trials, those levels achieved experimentally, and the numbers of eggs incubated in the subsamples of each trial (trials 5 and 6 are replicates at the design centre).

Trial	Design		Exptl levels ±1 SE		No. eggs, subsample			
	Salinity (‰)	Temp (C)	Salinity (‰)	Temp (C)	1	2	3	4
1	7.83	4.71	7.80±0.03	4.72±0.07	355	403	339	313
2	7.83	13.29	7.81±0.03	13.29±0.08	599	645	726	426
3	42.17	4.71	42.16±0.01	4.72±0.03	455	314	477	407
4	42.17	13.29	42.17±0.03	13.30±0.03	390	529	369	299
5	25.00	9.00	24.96±0.04	9.00±0.03	572	473	517	323
6	25.00	9.00	25.01±0.01	9.00±0.04	383	506	326	564
7	5.00	9.00	5.01±0.05	9.01±0.03	527	490	502	327
8	45.00	9.00	45.01±0.03	9.01±0.08	529	388	501	393
9	25.00	4.00	24.99±0.04	4.03±0.10	491	498	525	454
10	25.00	14.00	25.00±0.04	14.00±0.03	443	443	446	412
11	16.41	6.85	16.42±0.04	6.86±0.05	489	405	567	531
12	16.41	11.15	16.41±0.03	11.15±0.03	360	457	362	433
13	33.59	6.85	33.60±0.04	6.88±0.09	621	532	421	326
14	33.59	11.15	33.59±0.03	11.15±0.04	601	441	341	350

Response surface techniques were employed to describe the relation between salinity–temperature incubation conditions and larval length at median hatching time, percent total hatch, and percent viable hatch (Lindsey et al. 1970; Lindsey and Sandnes 1970). The fitting procedure employed either a linear polynomial

$$Y = b_0x_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2,$$

or the corresponding nonlinear form

$$Y^\gamma = b_0x_0 + b_1x_1^{\alpha_1} + b_2x_2^{\alpha_2} + b_{11}x_1^{2\alpha_1} + b_{22}x_2^{2\alpha_2} + b_{12}x_1^{\alpha_1}x_2^{\alpha_2},$$

where Y = response; x_1, x_2 = salinity (‰) and temperature (C), respectively; α_1, α_2, γ = power parameters derived by maximum likelihood procedure, depending on the results of the analysis.

Samples of about 250 larvae were taken from each incubator at the estimated time of maximum hatching frequency. The samples were submerged in closed containers of plastic and nylon mesh in their appropriate incubation tanks, and observed until death from starvation occurred. In two such tests (trials 1, 9) anomalies of the lower jaw were found in newly hatched larvae. These were discovered about 24 hr after hatching had begun, and their effects on subsequent development were not immediately determinable. In these trials, such larvae were included in counts of viable larvae, and they were so treated in the analyses. A correction was made later on the basis of subsequent development of the affected larvae.

Results

MORTALITY PATTERNS

In some of the trials, portions of the egg samples died prior to full-term development. In such instances, mortality usually was preceded by a lag or cessation in development. The time at which departure from a normal rate of development occurred was not clearly defined. In general, early mortality was noted among eggs developing in the three highest incubation salinities and temperatures. First indications appeared in trial 4 (42.17‰ S, 13.29 C); mortality estimated at 10% in the late gastrula stage rose to about 50% with the appearance of the optic capsules. Concurrently, in trial 10 (25.00‰ S, 14.0 C) and trial 2 (7.83‰ S, 13.29 C) a period of mortality occurred just prior to the beginning of eye pigmentation, resulting in mortality estimated as 50 and 15%, respectively. In trial 14 (33.59‰ S, 11.15 C) small losses were observed just prior to eye pigmentation, and the yolk sacs of remaining embryos had an unusual granular appearance. In trial 8 (45.00‰ S, 9.0 C) about 50% of the eggs died after the embryos had grown to encircle three-quarters of the yolk circumference and before the tail bud had begun to elongate. Finally, in trial 3 (42.17‰ S, 4.71 C) an estimated 80% of the eggs died between blastopore closure and beginning of eye pigmentation; the remainder died either just prior to or in the process of hatching. Prehatching mortality may be summarized as follows: between late gastrula and

establishment of the embryonic axis (trial 4); after blastopore closure and prior to eye pigmentation (trials 2, 3, 10, 12); just prior to and at hatching (trials 3, 10). Almost all remaining eggs in trial 3 died about 24 hr prior to the onset of hatching.

In addition, between the 1st and 4th day after hatching, there was a further period of mortality (60–80%) in the larval samples for trials 4, 8, 10, 13, and 14.

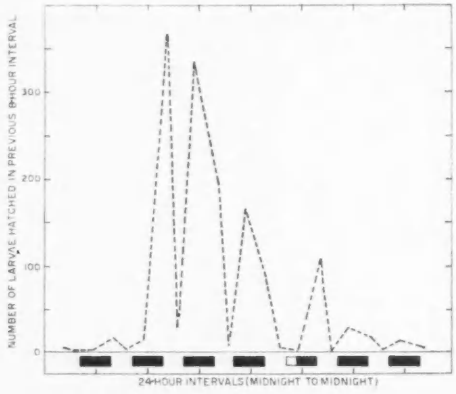

FIG. 1. Distribution of hatching in relation to hours of darkness (bars) in trial 5 (25.00‰ S, 9.0 C). The low rate of hatching at the beginning of the fifth dark interval occurred when the laboratory lights were left on; the same effect was noted in all other samples in the process of hatching.

RATE OF DEVELOPMENT

In all instances, hatching followed a daily cycle, apparently associated with light intensity. Although the 8-hr sampling periods were not synchronous with light and dark intervals, the majority of larvae hatching in each 24-hr period hatched in the hours of darkness between 5:00 PM and 7:00 AM (Fig. 1).

Duration of hatching periods was related to temperature, varying from about 137 hr at 14 C to 503 hr at 4 C (Table 2). Hatching distributions were positively skewed. Incubation times (fertilization to 50% hatch) were calculated on a logarithmic time scale, the daily hatching pulse necessitating a grouping of successive counts of hatched larvae into 24-hr intervals. Calculated times are based on the hatching of viable larvae; hatching frequency of abnormal larvae (spinal anomalies or curvature of body axis) tended to reach a maximum 1 or 2 days later than that of normal larvae. Incubation times ranged between 216.5 hr (42.17‰ S, 13.29 C) and 833.7 hr (25.00‰ S, 4.0 C). Rates of development ($\frac{1}{\text{days}} \times 100$) for the various incubation times (Table 2), along with other available data (Fujita and Kokubo 1927; Svetovidov 1952; McMynn and Hoar 1953; Outram 1955; Motoda and Hirano 1961; Taylor 1971), are compared with similar data for the Atlantic herring (Blaxter 1956) (Fig. 2).

Based on the current data, no clear relation can be seen between salinity and rate of development. However, two observations suggest that minor *apparent* differences in rate of development

TABLE 2. Duration of hatching period, incubation time (fertilization to 50% hatch), and rate of development of Pacific herring eggs incubated under the test conditions.

Trial	Test conditions: Salinity (‰)	Test conditions: Temp (C)	Duration of hatching interval (*hr*)	Incubation time (*hr*)	Rate of development (%/*day*)
1	7.83	4.71	359.1	674.8	3.56
2	7.83	13.29	156.6	217.0	11.06
3	42.17	4.71	–	–	–
4	42.17	13.29	133.0	216.5	11.09
5	25.00	9.00	239.4	354.8	6.76
6	25.00	9.00	246.2	390.6	6.14
7	5.00	9.00	251.7	344.8	6.96
8	45.00	9.00	272.5	377.2	6.36
9	25.00	4.00	503.3	833.7	2.88
10	25.00	14.00	137.2	222.1	10.81
11	16.41	6.85	345.9	517.8	4.63
12	16.41	11.15	198.9	273.9	8.76
13	33.59	6.85	345.6	502.9	4.77
14	33.59	11.15	215.8	286.4	8.38

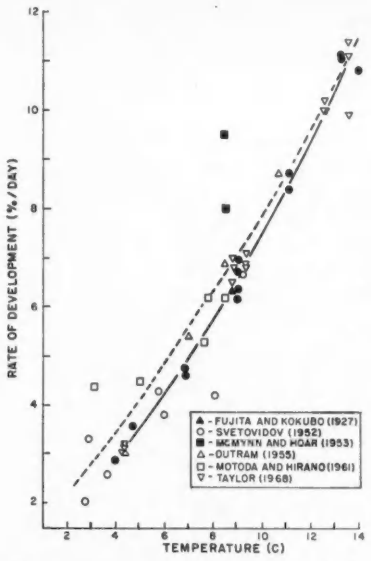
RATE OF DEVELOPMENT (%/DAY)
TEMPERATURE (C)
▲ - FUJITA AND KOKUBO (1927)
○ - SVETOVIDOV (1952)
■ - McMYNN AND HOAR (1953)
△ - OUTRAM (1955)
□ - MOTODA AND HIRANO (1961)
▽ - TAYLOR (1968)

FIG. 2. Effects of temperature at various salinities on rate of development of Pacific herring eggs. The solid trend line is calculated from the current data (solid circles; see text). The dotted trend line compares similar data (Blaxter 1956) for the Atlantic herring (for "▽" data see Taylor 1971).

might occur if salinity is near the limit of tolerance. In the two trials (1 and 3) at 4.71 C (7.83 and 42.17‰ S), rates of development were identical until the embryos had grown to encircle the yolk about 1.25 times. Thereafter, development decelerated in 42.17‰ S, followed by death of the embryos. In the three trials (5–8 inclusive) at 9.0 C (5.0, 25.0, and 45.0‰ S), rates of development and initiation of hatching were almost identical. However, hatching in 45.00‰ S was more protracted. It appeared that the small weak larvae produced may have had more difficulty hatching, thereby prolonging the process. Thus, some differences in hatching times may reflect the quality (or state of development) of embryos at hatching time, rather than an adjustment of rate of development in response to external salinity.

The relation between temperature and rate of development (solid trend line, Fig. 2) may be approximated by

$$Y = 0.7648 + 0.4367x_1 + 0.0235x_1^2,$$

where Y = rate of development (%/day); x_1 = temperature (C).

CONDITION OF LARVAE

Newly hatched larvae were very active and swam normally, with the following exceptions. Larvae from trial 7 (5.0‰ S, 9.0 C) were normal in appearance but inactive; they lay motionless on the bottom of the container, individual larvae showing occasional short bursts of activity. Larvae from trial 9 (25.0‰ S, 4.0 C) initially were relatively inactive, but became more active with increasing development. Larvae from trial 8 (45.0‰ S, 9.0 C) were small and relatively inactive; they had small, bulbous, yellowish-coloured yolk sacs similar to those described for Atlantic herring larvae incubated at high salinities (Holliday 1969 p. 305–306). In salinities of 33.59‰ or greater, larvae were buoyant.

In two trials, newly hatched larvae were characterized by a complete absence of the lower jaw (trial 1, 7.83‰ S, 4.71 C) or by its retarded development (trial 9, 25.00‰ S, 4.0 C). In trial 9, many larvae subsequently developed lower jaws that were normal in appearance. However, subsequent development in trial 1 larvae was abnormal in most instances, the head being bent downward and the lower jaw widely agape at all times (Fig. 3). Feeding behaviour was noted ultimately in all trials except that at 7.83‰ S, 4.71 C.

SIZE OF LARVAE

Estimates of mean total length were obtained for successive samples of newly hatched larvae taken at 8-hr intervals throughout the greater part of each hatching period. Considerable scatter occurred in these series of means. Nevertheless, in 12 of the 13 trials in which larvae were obtained, size of larvae tended to increase from the onset of hatching, reach a maximum, and decline in later samples. In the remaining trial (7.83‰ S, 4.71 C), length of newly hatched larvae increased constantly throughout the initial 98% of the hatching period examined.

Objective estimates of larval length were obtained as follows. A second order polynomial was fitted to each series of mean lengths. From these fitted relations, estimates were derived of total length at median hatching time (Table 3). Representative sets of means of larval length, from whose distributions (Fig. 4) the tabled values were obtained, illustrate the following relations.

At higher incubation temperatures, maximum total length tends to occur at or near the median hatching time. At lower temperatures, maximum length is reached later in the hatching distribution, after the median hatching time (cf. 25.0‰ S; 14.0, 9.0, 4.0 C). This "uncoupling" of maximum hatching frequency and maximum larval size is

accentuated at combined low temperatures and low salinities (trial 1, 7.83‰ S, 4.71 C).

In addition, mean larval length at median hatching time is greater at lower temperatures (cf. 25.0‰ S; 14.0, 9.0, 4.0 C) and at lower salinities (cf. 9.0 C; 5.0, 25.0, 45.0‰ S). Increased water content of larvae at lower salinities could possibly account for the observed differences in length in the same way that salinity affects wet weight (Holliday 1965). However, calculated larval length at median hatching time in trial 11 (16.41‰ S, 6.85 C) is greater than expected, either on the basis of salinity or temperature alone. Thus, total length is maximized at a combination of intermediate salinity and temperature levels near that of trial 11, and the maximum cannot be considered as a simple function of body water content.

Concomitant series of measurements of mean yolk sac length (Fig. 4) show considerable scatter, yet suggest several trends. The inverse relation suggested between salinity and mean yolk sac length at median hatching time in the three trials at 9.0 C (5.0, 25.0, 45.0‰ S) again probably reflects an increased water content of larval structures at lower salinities. There also appears to be a tendency for yolk sac size at median hatching time to be greater at lower temperatures (cf. 25.0‰ S; 14.0, 9.0, 4.0 C).

The relation of larval size at median hatching time to incubation levels of salinity (x_1) and temperature (x_2) acting in concert was calculated by response surface techniques. Hence, using the nonlinear polynomial as a model

$$Y^{-1.270} = 0.0910 + 1.7184 \times 10^{-3}x_1^{0.635} - 0.2625x_2^{-0.767} + 3.4568x_1^{1.270} + 0.7824x_1^{-1.534} - 0.0236x_1^{0.635}x_2^{-0.767},$$

where Y = total length (mm); α_1, α_2, γ = 0.6349, −0.7669, −1.2700 respectively. The relative likelihood of the analogous linear model ($\alpha_1 = \alpha_2 = \gamma = 1$) adequately representing the data, compared with the nonlinear solution given,[1] is 1.90×10^{-2}. The nonlinear model is retained, the maximum likelihood solution is considered as providing the best available estimates of the β coefficients and power parameters. Analysis of variance, given the data and the model, indicated that none of the terms in the fitten polynomial could be omitted without seriously affecting the adequacy of the model. The canonical equation of the resulting response surface (Fig. 5) is

$$Y' - 6.147 \times 10^{-2} = 0.78262Z_1^2 + 1.6740 \times 10^{-4}Z_2^2,$$

where Y′ = total length (mm) in terms of Y^γ; $0.006147 = Y_s^\gamma$, response at S, the centre of the surface; Z_1, Z_2 = conical variables.
Maximum larval length, 8.99 mm, is calculated to occur at (20.00‰ S, 5.54 C).

The surface illustrates the interaction between salinity and temperature; near-maximum larval size is attained on a ridge running from combinations of high salinity and low temperature to those of low salinity and high temperature (high/low–low/high interaction). However, the location of s, the centre of the surface on this ridge, is not known with precision.[2]

The most plausible estimate is retained (20.00‰ S, 5.54 C), recognizing that the location of S is somewhere on the ridge of near-maximum larval size, probably at a temperature near 5.5 C. In general, near-maximum larval size is obtained over a wide range of salinities (about 5–35‰) but is confined to a relatively narrow range of temperatures (about 4.5–8 C), and there is an inverse relation between salinity and temperature as they affect larval size.

Total Hatch

Total hatch varied between a minimum of 1.36% (trial 3) and a maximum of 93–94% (trials 1, 9, 11) (Table 3). Analysis in terms of the nonlinear model found no unique solution superior to the analogous linear case ($\alpha_1 = \alpha_2 = \gamma = 1$). Hence

$$Y = 80.2033 + 0.1287x_1 + 5.7938x_2 - 0.0691x_1^2 - 0.6691x_2^2 + 0.2370x_1x_2,$$

where Y = total hatch (%).

Analysis of variance based on the linear model indicated that the experimental treatments explain a large portion of the variance, and that the linear term for salinity (x_1) could be omitted from the polynomial without seriously affecting the adequacy of the model. Although a significantly large portion of the variance attributed to treatments is not explained by regression on the x_1, $\cdots$, x_1x_2 com-

[1]Ratios equal to or greater than 0.1 may be compared with a 95% probability interval for a normal theory linear model (Lindsey 1970). Hence, in this instance, the linear solution is considered implausible.

[2]Lack of precision in determination of S is shown by the likelihood graphs of other values for its salinity and temperature components: other plausible estimates range between temparatures of 3 and 6 C over the range of salinities examined.

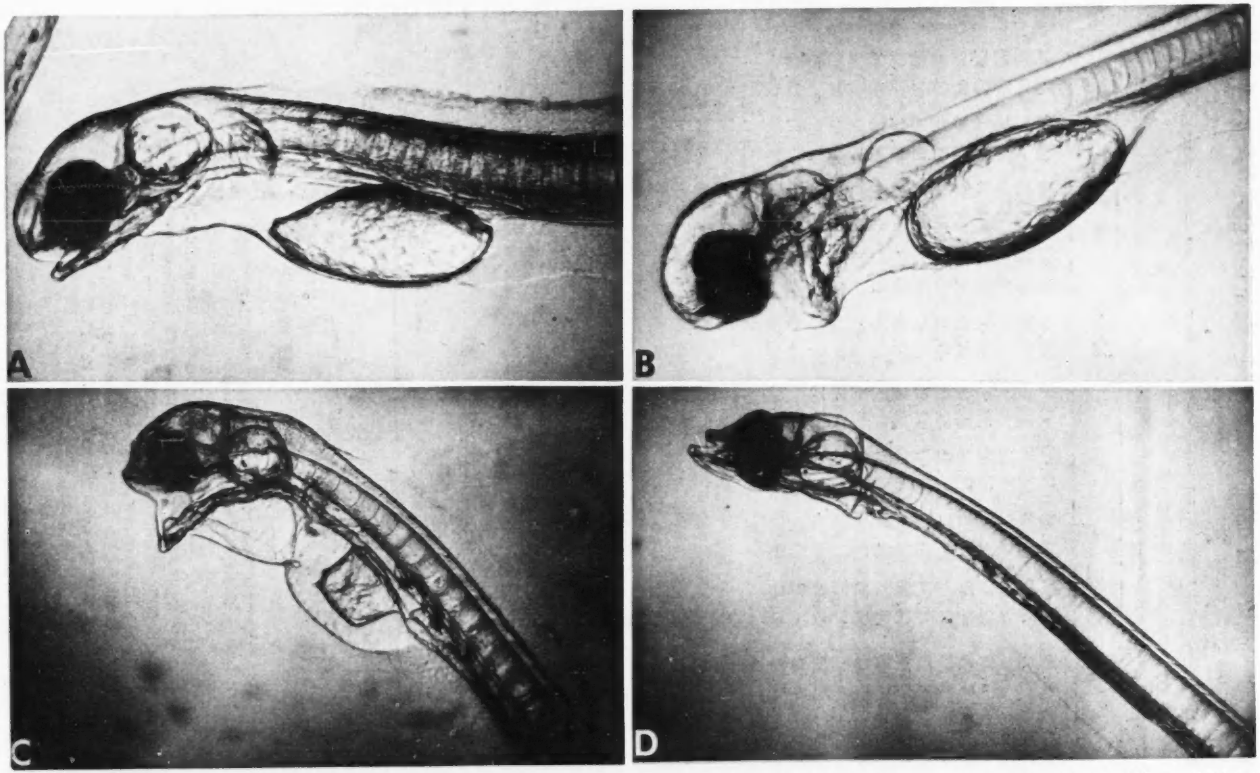

FIG. 3. Effects of temperature on development of lower jaw. (A) 25.00‰ S, 4.0 C, trial 9; (B, C) 7.83‰ S, 4.71 C, trial 1; (D) 16.41‰ S, 6.85 C, trial 11. (A) One-day-old larva hatched at median hatching time; jaw development near normal, more advanced than in larvae hatching earlier in trial; (B) newly hatched larva, hatching at median hatching time. Note rudimentary lower jaw; (C) 7-day-old larva. Note decurved head and fixed gape of jaws; (D) 19-day-old larva, normal development. In trial 9 the majority of larvae alive at yolk absorption developed as in (D); very few such normal larvae were produced in trial 1.

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TABLE 3. Calculated total length of larvae at median hatching time, percent total hatch, and percent viable hatch of Pacific herring eggs under the given experimental conditions.

Trial	Incubation Salinity (‰)	Incubation Temp (C)	Total length (mm)	% total hatch in subsample 1	2	3	4	Mean	% viable hatch in subsample 1	2	3	4	Mean
1	7.83	4.71	8.25	96.90	94.04	94.40	92.33	94.41	71.27	81.89	64.90	61.34	69.85
2	7.83	13.29	8.05	73.79	76.28	61.16	82.63	73.46	69.45	69.77	54.13	77.23	67.64
3	42.17	4.71	–	3.74	0.32	0.42	0.98	1.36	0.00	0.00	0.00	0.00	0.00
4	42.17	13.29	6.48	62.82	46.31	68.02	39.13	54.07	47.18	34.40	51.49	25.42	39.62
5	25.00	9.00	7.89	68.88	86.05	78.14	82.04	78.77	66.26	84.57	74.85	79.88	76.39
6	25.00	9.00	8.53	91.64	85.77	95.71	84.04	89.29	88.25	81.42	91.72	78.01	84.85
7	5.00	9.00	8.77	71.54	86.53	82.67	93.88	83.65	68.50	83.88	78.69	92.66	80.93
8	45.00	9.00	7.19	44.80	58.51	48.10	50.13	50.38	30.25	52.58	39.32	36.13	39.57
9	25.00	4.00	8.68	93.28	94.78	92.57	92.07	93.17	83.50	87.15	78.86	83.26	83.19
10	25.00	14.00	7.44	69.30	63.66	56.95	60.68	62.64	54.40	56.43	45.07	51.46	51.84
11	16.41	6.85	8.85	90.39	97.04	95.94	93.97	94.33	88.75	95.06	90.30	90.40	91.12
12	16.41	11.15	8.36	89.44	85.12	92.82	77.83	86.30	85.00	82.28	87.57	72.98	81.95
13	33.59	6.85	8.29	92.43	80.08	83.37	90.49	86.59	85.35	76.50	75.30	86.20	80.83
14	33.59	11.15	7.06	70.72	93.20	80.06	79.43	80.85	65.06	87.76	73.90	70.29	74.25

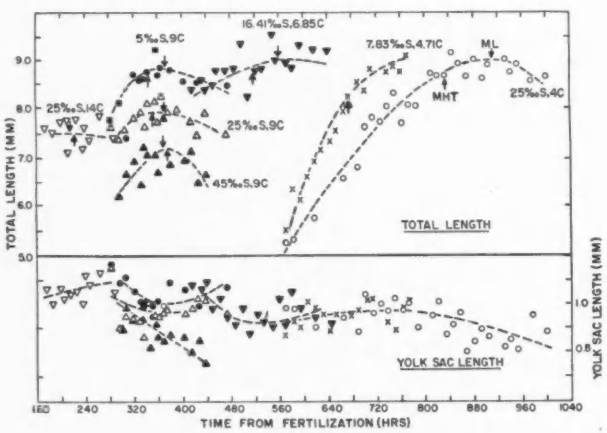

FIG. 4. Mean size of larvae sampled at intervals throughout the hatching period (upper set of curves). On the curves: upper arrows — calculated maximum length achieved; lower arrows — calculated length at median hatching time (e.g., ML and MHT, respectively; 25.00‰ S, 4.0 C curve). The lower set of curves illustrates concurrent measurements of antero-posterior yolk sac length.

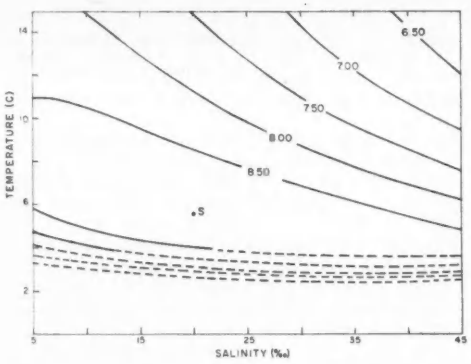

FIG. 5. Calculated isopleths of total length of larvae (mm) at median hatching time in relation to salinity and temperature incubation conditions. Maximum size is estimated to occur at *S*, the centre of the surface, which lies on a ridge of near-maximum length extending from temperatures near 4 C at higher salinites to temperatures near 8 or 9 C at lower salinities.

ponents of the model, the β coefficients so obtained are retained as the best available estimates. The canonical equation of the resulting response surface (Fig. 6) is

$$Y - 99.68 = -0.6917Z_1^2 - 0.4651Z_2^2,$$

where Y = total hatch (%); 99.68 = Y_s, response at *S*, the centre of the surface; Z_1, Z_2 = canonical variables.

Maximum percent total hatch is calculated to occur at (12.01‰ S, 6.46 C).

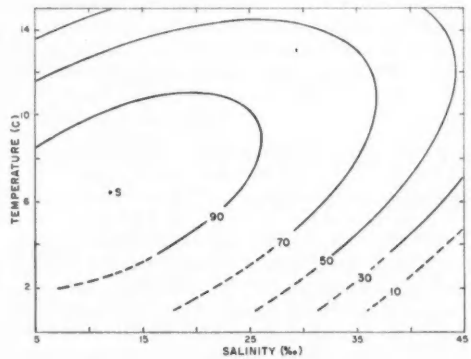

FIG. 6. Calculated isopleths of percent total hatch in relation to salinities and temperatures of incubation. Maximum percent total hatch is calculated to occur at *S*.

The surface illustrates a low/low–high/high interaction between salinity and temperature. For example, maximum potential total hatches in lower salinities would be found at lower temperatures. Comparison with the surface for larval size (Fig. 5) indicates that both maximum total hatch and largest larvae are to be expected at incubation salinities and temperatures near those of trial 11 (16.41‰ S, 6.85 C). However, the surface contours for percent total hatch (Fig. 6) are constrained by the model and their centre is also estimated with low precision (other plausible estimates of the levels of salinity and temperature at *S* range between 0–17‰ S and 0–8 C). Nevertheless, the nature of the interaction suggests that near-maximum percent total hatches, at salinities higher than that at *S*, would be found at higher temperatures, conditions that would produce smaller larvae.

VIABLE HATCH

Viable hatch varied from zero (trial 3) to a maximum of about 91% (trial 11) (Table 3). As in the previous instance, no unique solution could be obtained by response surface analysis superior to that provided by the linear model. Hence

$$Y = 22.7560 + 1.5441x_1 + 13.8280x_2 - 0.0787x_1^2 - 0.9684x_2^2 + 0.1356x_1x_2,$$

where Y = viable hatch (%).

Analysis of variance indicated that the experimental treatments explain a large portion of the variance, and that the linear term for salinity (x_1) could be eliminated without seriously affecting the adequacy of the model. However, as in the analysis of percent total hatch, the portion of the treatment variance not explained by regression on the terms of the linear model is greater than to be expected by chance alone. Since the linear model provides constrained estimates of contours around the centre of the surface (Lindsey et al. 1970), the contours constructed for both percent total and viable hatch should be regarded as general approximations of surface structure. The canonical equation of the surface for percent viable hatch (Fig. 7) is

$$Y - 93.46 = -0.9735Z_1^2 - 0.0736Z_2^2,$$

where Y = viable hatch (%); 93.46 = Y_s, response at *S*, the centre of the surface; Z_1, Z_2 = canonical variables.

Maximum percent viable hatch is calculated to occur at (16.98‰ S, 8.33 C).

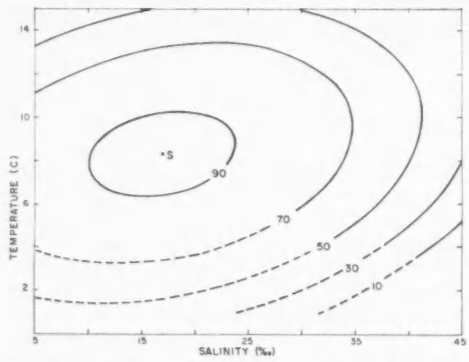

FIG. 7. Calculated isopleths of percent viable hatch in relation to salinities and temperatures of incubation. Maximum percent viable hatch is calculated to occur at *S*.

The surface for percent viable hatch is similar to that for percent total hatch; a low/low–high/high interaction between salinity and temperature is indicated. The centre of the surface, however, is estimated with greater precision. Relative likelihood graphs of salinity and temperature around their maximum likelihood estimates at *S* provide plausible ranges between 13–19‰ S and 7.6–8.7 C.

POSTHATCHING OBSERVATIONS

Among the samples of larvae held after hatching, the following observations were noted (in order of decreasing temperature).

Trial 10 (*25.00‰ S, 14.0 C*): Substantial numbers of deformed and dead larvae in first 4 days, although less than in trial 4. Survivors developed into vigorous larvae, normal in appearance.

Trial 4 (*42.17‰ S, 13.29 C*): Estimated 80% mortality in first 4 days. Survivors appeared normal.

Trial 2 (*7.83‰ S, 13.29 C*): No mortality in first 4 days, larvae normal in appearance.

Trial 14 (*33.59‰ S, 11.15 C*): Estimated 60–70% mortality in first 2 days. Survivors normal in appearance.

Trial 12 (*16.41‰ S, 11.15 C*): No mortality in first 4 days. Normal larvae.

Trial 8 (*45.00‰ S, 9.0 C*): Estimated 75% mortality in first 24 hr. Larvae weak in appearance with dense, "crystalline"-appearing, bulbous yolk sacs. Survivors seemed normal but small; chromatophores small and inconspicuous, either contracted or poorly developed, in comparison with larvae in other samples.

Trial 6 (*25.00‰ S, 9.0 C*): No mortality in first 4 days, normal larvae.

Trial 7 (*5.00‰ S, 9.0 C*): Estimated 90% mortality in first 3 days. Larvae virtually inactive.

Trial 13 (*33.59‰ S, 6.85 C*): Estimated 70–80% mortality in first 2–4 days. Survivors normal in appearance.

Trial 11 (*16.41‰ S, 6.85 C*): Virtually no mortality in first 4 days; normal larvae (Fig. 3D).

Trial 3 (*42.17‰ S, 4.71 C*): No normal, live larvae obtained.

Trial 1 (*7.83‰ S, 4.71 C*): Lower jaw absent in all larvae at hatching. Lower jaw developed in next 8 days but most larvae (90%) considered inviable; head bent ventrally and lower jaw fixed agape (Fig. 3B, C).

Trial 9 (*25.00‰ S, 4.0 C*): Retarded development of lower jaw at hatching: subsequent development in next 8 days, appeared normal. A limited number of larvae, normal in appearance, survived to yolk sac absorption and starvation (Fig. 3A).

These observations may be summarized as follows. Mortality, or presence of inviable larvae, *in the first 4 days after hatching*, was:

- either very low or absent in salinities between 16.41 and 25.00‰, and in temperatures between 6.85 and 11.15 C (trials 5, 6, 11, 12). However, at the stage of yolk exhaustion, total mortality was lowest in trial 11 (16.41‰ S, 6.85 C) and trial 12 (16.41‰ S, 11.15 C).
- high in salinities of 33.59‰ or greater, at all temperatures tested (trials 3, 4, 8, 13).
- high in 5.0‰ S (at 9.0 C, trial 7). This is probably an effect of low salinity, as mortality was absent in a slightly higher salinity (7.83‰) at a higher temperature (trial 2), and in a higher salinity (25.00‰) at the same temperature (trials 5, 6).
- high in temperatures of 4.71 C or lower, at all salinities tested (trials 1, 3, 9).
- high in temperatures of 13.29 C or greater, in salinities of 25.00‰ or greater (trials 4, 10).

Observations were also made on the beginning of feeding behaviour, yolk exhaustion, noticeable decline in feeding motions, beginning of morbidity from starvation, final maximum length achieved and time to complete mortality (Table 4).

Discussion

EXPERIMENTAL RESULTS

As a basis for discussing the experimental results, the hypothesis is examined that incubation conditions most favourable to developing eggs are those providing the greatest numbers of viable larvae of largest size in the shortest incubation period. It is also reasoned that such conditions most likely would be met if maximum size occurred at the time of maximum hatching frequency — when maximum size would apply to the majority of larvae in a sample. It is assumed that these

TABLE 4. Observations on groups of approximately 250 Pacific herring larvae sampled at the median hatching time and returned to the incubation tanks. No external food source provided.

			Observed no. days from hatching until						Estimated viable larvae (% of original egg samples)		
Trial	S (‰)	Temp (C)	Feeding behaviour noted	Yolk exhausted	Feeding behaviour diminishing or activity decreasing	Initial deaths from starvation	All dead	Maximum length of larvae attained (*mm*)	At hatching	4 days after hatching	At exhaustion of yolk
1	7.83	4.71	–[a]	16	18	18	29	9.4–9.8	70	7[b]	2
2	7.83	13.29	4	4	9	12	14	9.4	68	64	64
3	42.17	4.71	–	–	–	–	–	–	0	0	0
4	42.17	13.29	4	5	9	9	10	9.4–9.8	40	4	4
5,6	25.00	9.00	4	6	13	17	23	9.8–10.7	76	68	65
7	5.00	9.00	6[c]	8	10[c]	10	12	9.0–9.8	81	6	5
8	45.00	9.00	4	8	12	–[d]	16	8.6–9.4	40	6	1
9	25.00	4.00	8	12	23	25	31	10.3–11.1	83	80	30[e]
10	25.00	14.00	3	4	11	13	15	9.4–9.8	52	21	21
11	16.41	6.85	3	5	9	19	24	9.8–10.7	91	90	79
12	16.41	11.15	4	6	11	15	17	9.8	82	80	78
13	33.59	6.85	4	6	10	16	20	9.8–10.7	81	18	15
14	33.59	11.15	4	6	11	15	19	9.8–10.7	74	24	24

[a]None observed.
[b]All alive; figure based on later estimate that 10% of larvae were viable.
[c]Very inactive; few feeding motions.
[d]Mortality continuous after hatching.
[e]Based on later estimate that 90% of surviving larvae viable.

circumstances would: (*a*) minimize the passive period of egg development, potential egg loss from predation, and physical damage from adverse weather conditions, while (*b*) producing larger larvae with improved chances of capturing food organisms, resulting in more rapid growth to larger sizes less susceptible to initial periods of mortality. The various findings are summarized in Fig. 8 for examination in relation to the hypothesis.

RATE OF DEVELOPMENT

The available data associated with rate of development suggest that British Columbia herring eggs may require somewhat higher temperatures for successful development than eggs from other stocks in Asian waters (e.g., fig. 2 Svetovidov 1952). Development of Pacific herring eggs also appears to be slower at lower incubation temperatures than that of Atlantic herring eggs. The latter have also been incubated at temperatures as low as 2.3 C (see Blaxter 1956). It would be of interest to compare, by similar criteria, the viability of Pacific herring eggs, incubated at temperatures between about 2 and 5 C, from other regions over the range of geographic distribution.

EGG SURVIVAL

In general, the developing eggs showed a high degree of plasticity with respect to the various incubation conditions employed. In 12 of the 14 trials at least 40% of the eggs produced viable larvae. Salinities and temperatures associated with the 90% isopleth of viable hatch (Fig. 8) range from about 10 to 24‰ S and from 6.5 to 10.5 C. On this basis, the Pacific herring egg is considered euryhaline and stenothermal (Kinne 1963, 1964; Alderdice 1971).

The calculated centres of percent total hatch (12.01‰ S, 6.46 C) and viable hatch (16.98‰ S, 8.33 C) suggest that egg survival is enhanced by incubation at intermediate salinities. These conclusions are in agreement with the results of McMynn and Hoar (1953), who concluded that salinities associated with optimum development of Pacific herring eggs ranged between their test levels of 11.53 and 16.24‰ S.

By comparison, survival of Atlantic herring eggs is improved in sea water of reduced salinity, with a maximum near 20–25‰ S (Holliday and Blaxter 1960). Holliday and Jones (1965) showed eggs and

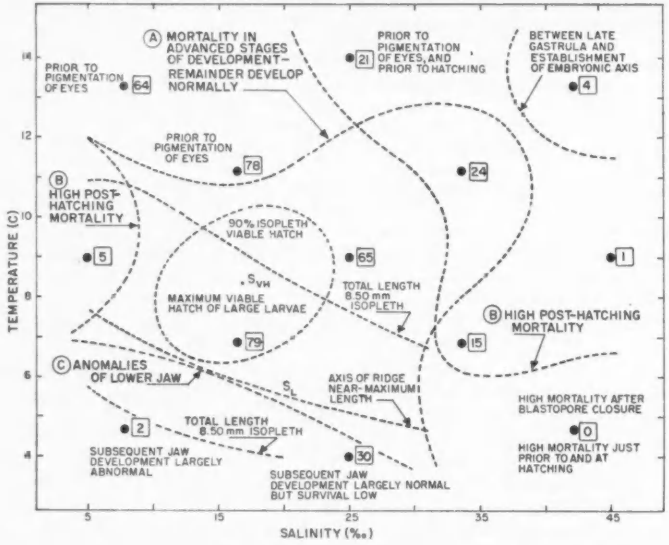

FIG. 8. Summary of effects of salinity and temperature on development of Pacific herring eggs, and on larvae existing on yolk stores. The array of solid circles locates the experimental trials. The boxed figures at each trial estimate the percentage survival of eggs producing viable larvae alive at time of yolk sac absorption. Areas of the salinity–temperature test space are shown, within which the following observations were noted: (A) mortality at various stages of embryonic development; (B) mortality in the 4-day period after hatching; (C) anomalous development of lower jaw. Maximum larval size at median hatching time (S_L) is shown on the ridge of near-maximum larval size, which is bounded by total length isopleths of 8.50 mm. The 90% isopleth of viable hatch is shown with its centre at S_{VH}.

blood of this species to be osmotically equivalent to salinities of 12.50 and 15.33‰, respectively. Least osmotic adjustment of the yolk of Atlantic herring eggs throughout development appears to be obtained at an external salinity near 17.5‰ (Holliday and Jones 1965). After gastrulation, the whole egg is regulated to a value equivalent to 12‰ or somewhat greater, depending on the external salinity (Blaxter and Holliday 1963 p. 272). Newly hatched larvae from eggs incubated at salinities of 10.9–47.8‰ were shown to have body fluid osmotic concentrations of 10.7–13.7‰ (as NaCl) (Holliday and Blaxter 1960). It is assumed that the relation between intermediate salinities, survival, and osmotic regulation in the Atlantic species would find analogies in the Pacific herring.

LARVAL SURVIVAL

About 65% or more of the eggs in trials 2, 5, 6, 11, and 12 produced larvae that lived to yolk sac absorption. These trials represent salinity and temperature ranges of 7.83–25.00‰, and 6.85–13.29 C. Although high survival to hatching occurred in a number of trials, total survival of viable larvae to yolk absorption remained highest at a salinity of 16.41‰ in temperatures of 6.85 C (trial 11) and 11.15 C (trial 12).

McMynn and Hoar (1953) considered salinity tolerance of Pacific herring larvae to range from about 6.06 to 34.28‰ S. Kurata (1959) tables data suggesting that larvae in Japanese waters can tolerate (after 19 days exposure) salinities ranging from 30 to 130% sea water (about 10–42‰ S) with a possible optimum near 70% (22.6‰ S). Fujita and Kokubo (1927) concluded that Japanese herring larvae survived best in four-fifths normal sea water (25.8‰ S), followed by survivals in lower salinities to $\frac{1}{10}$ normal sea water.

By comparison, Atlantic herring larvae have a high capacity for osmotic regulation when transferred to other salinities within their range of tolerance (Blaxter and Holliday 1963). Larvae regulated

their tissues to the equivalent of salinities of 9.8–15.0‰ when transferred to salinities ranging from 2.5 to 52.5‰. The comparison in ranges of salinity tolerance of the two species suggests that Pacific herring larvae may also be capable of effective osmotic regulation of tissues over a somewhat smaller, although still wide range of salinities. Nevertheless, as in the case of incubating eggs, yolk sac larvae appear to survive best at intermediate salinities near 16.41‰ (trials 11, 12).

Anomalies of the Lower Jaw

In the higher incubation temperatures, gross observations indicated that development of the lower jaw proceeds in a manner comparable to that in the Atlantic herring. At hatching time the lower jaw is normally shorter than the upper jaw. In succeeding days it grows to project forward beyond the upper jaw. In trials 1 (7.83‰ S, 4.71 C) and 9 (25.00‰ S, 4.0 C), however, the lower jaw was entirely absent at hatching or rudimentary in form.

Evidence based on development of Atlantic herring larvae suggests that the period between hatching and the establishment of feeding on external food sources is a critical one (Blaxter 1965). Feeding behaviour, involving S-shaped flexure of the body (Rosenthal 1969a), begins soon after hatching. The success of this prey-capturing reaction is related to the time at which the behaviour is initiated, while its frequency may be reduced by unsuccessful prey-capturing attempts. Rosenthal (1969a, b, personal communication) concludes for the Atlantic herring that: efficiency of utilization of captured food is low in the initial stages of prey-catching behaviour; if food is withheld from the herring larvae, and is not presented before approximately the time of 50% yolk absorption, the learning process leading to improved prey-capturing accuracy may result in a rate of food intake insufficient to provide minimum requirements for continued growth and development. Extending these arguments to Pacific herring larvae, it is assumed that larvae from the low temperature trials (trials 1, 9) could be subject to a problem mitigating against their ability to develop a normal sequence of feeding behaviour. No S-shaped feeding motions were observed among larvae from trial 1 (7.83‰ S, 4.71 C). Subsequent development of the lower jaw appeared normal in the majority of survivors in trial 9 (25.00‰ S, 4.0 C). However, the question remains as to whether or not development of the lower jaw and subsequent appearance of feeding behaviour (Table 4) would have occurred in time for food-gathering capacity to satisfy energy requirements for continued growth. Thus, the presumed advantage of large size in larvae hatching from temperatures of about 4–5 C could be offset not only by decreased survival noted in the trials, but also by a suspected interference with normal development of feeding behaviour and prey-capturing ability among the survivors.

Size of Larvae

Pacific herring larvae at hatching tended to be longer at lower incubation temperatures, an observation noted for a number of species (Blaxter 1969). However, the *range* of sizes produced also increased at lower temperatures, some of those larvae being considerably smaller than the smallest larvae obtained at higher temperatures (Fig. 4). Moreover, maximum size attained at hatching in low temperatures may apply only to those larvae hatching late in the hatching interval and not to the majority of larvae produced at or near the median hatching time.

Larger larvae were also produced at lower salinities (Fig. 4). However, the differences in size attributed to salinity would be influenced by osmotic relations, the larvae at lower salinities presumably having a higher water content. Holliday and Blaxter (1960) incubated Atlantic herring eggs at salinities ranging from 5.9 to 52.5‰ (at 11.2–11.7 C). Their results suggest a curvilinear increase in length and a linear increase in wet weights of newly hatched larvae, the maximum in each instance occurring in the lowest incubation salinity. However, in the present instance, *ultimate* maximum size at median hatching time, in terms of both salinity and temperature, appears to be achieved at intermediate salinities and at a temperature several degrees Celsius higher than might be expected on the basis of temperature alone. The possibility also exists that conversion of yolk into larval tissue may be more efficient, either per unit time within the incubation period or in terms of tissue produced, at those incubation conditions providing maximum size in a majority of larvae. Confirmation would require further information, such as dry weights of larvae and yolk sac contents, associated with development in various salinity–temperature conditions.

The calculated incubation conditions related to ultimate maximum larval size at median hatching time (20.00‰ S, 5.54 C) occur on a ridge of near-maximum larval size (Fig. 8). This salinity–temperature locus was derived with low precision; other less likely but still plausible solutions would place the centre somewhere on the salinity ridge at a temperature between 3 and 6 C. However, evidence was presented in the previous section indicating that low survival of larvae to yolk absorption

might be anticipated at temperatures below about 5 C. Moreover, both the calculated centre of maximum larval size and ridge of near-maximum size (Fig. 8) are seen to lie outside the 90% isopleth for viable hatch. As indicated previously, other less likely but still plauxible estimates of the components of the centre for percent viable hatch range between 13 and 19‰ S, and 7.6 and 8.7 C. Therefore, it appears that salinity–temperature incubation conditions resulting in maximum larval size are not the same as those associated with maximum percent viable hatch.

Hence, to allow simultaneous consideration of larval size and percent viable hatch, isopleths of 8.50 mm total length have been selected arbitrarily (Fig. 8), representing salinity–temperature incubation conditions associated with about 95% of maximum calculated larval size. In this manner, an intersection of the two surfaces is defined that encloses those incubation conditions associated with *both* near-maximum larval size *and* near-maximum percent viable hatch. The intersection of the surfaces reduces the ranges of salinities and temperatures considered, from those associated with the two variates separately, to about 10–23‰ S and 6.5–9.5 C.

In spite of the differences in mortality of prehatching and posthatching stages observed in the various trials, all surviving larvae reached a total length of about 10 mm on available yolk stores (Table 4). Slightly larger larvae at yolk absorption was noted in trials 5, 6, 9, 11, 13, and 14, those experiencing salinities and temperatures between 16.41 and 33.59‰ S and 4 and 11.15 C. Somewhat smaller size at yolk absorption occurred in trials 1, 2, 4, 7, 10, and 12, those incubations involving low salinities, low salinities and high temperatures, or high temperatures. Thus, even though larval size at median hatching time was reasonably high in low salinities (trials 1, 7), advantages either in terms of size or survival were not retained to yolk absorption. Large larvae at yolk absorption also were produced at 4 C (trial 9), yet relatively few larvae survived to that stage. Finally, maximum survival to yolk absorption was confined to larvae in trials 11 and 12, and maximum survival to yolk absorption of largest larvae occurred in trial 11 (16.41‰ S, 6.85 C).

In summary, incubation conditions providing maximum viable hatch of largest larvae are interpreted as those enclosed within the intersection of the surfaces in Fig. 8. This salinity–temperature space also encloses the trial (16.41‰ S, 6.85 C) at which was achieved both maximum production of largest larvae at hatching, and maximum survival of viable larvae of near-maximum size. The centre of the surface for percent viable hatch (16.98‰ S, 8.33 C) is assumed to be a reasonable approximation of these optimum conditions. In addition, around this centre and within the intersection, incubation periods would be shorter at the higher temperatures. The highest plausible temperature in this regard is taken as 8.7 C, the upper temperature limit in the likelihood graphs of the components of the centre for viable hatch (13–19‰ S, 7.6–8.7 C). Therefore, for the Pacific herring the hypothesis is advanced that maximum numbers of viable larvae, of largest size at median hatching time, produced in the shortest incubation period, and reaching near-maximum size at the stage of yolk absorption in greatest numbers, would be produced by incubation conditions at or near 16.98‰ S and 8.7 C.

Ecological Implications

It remains to be discovered whether or not the data and interpretations of the foregoing sections conform with observations obtained by field investigation. In making this comparison it is recognized that, besides salinity and temperature, numerous other biotic and abiotic factors can influence survival under natural conditions, and that these may not have been operating in the relatively simple laboratory environments employed. Such other factors could influence egg and larval survival directly or indirectly, and could modify the experimental results obtained with respect to salinity and temperature. Hence, ecological interpretation of experimental data must be undertaken with caution. For the Pacific herring, as for many other marine fishes (Blaxter and Holliday 1963 p. 371), this problem is magnified by the limited amount of information available, either from field or experimental studies, on the physiology and behaviour of the species.

Studies related to exploitation of herring have demonstrated the presence of semi-isolated spawning stocks or subpopulations (Motoda and Hirano 1961; Taylor 1964). If partially restricted gene pools occur over the range of distribution of the Pacific herring, the potential for physiological or behavioural differentiation of subpopulations is also assumed to exist. Unfortunately, those characteristics of different spawning stocks that have been recorded — salinities and temperatures or times of spawning, growth rates, mortality rates, or meristic characteristics — generally do not allow a distinction to be made between biological causes and environmental consequences of subpopulation separation. The results of the current study refer to eggs from one subpopulation (Vancouver Island

lower east coast; Taylor 1964). Discussion of these results, relative to the geographic range of the species, does not preclude the possibility that differences in physiological characteristics of salinity or temperature tolerance may occur between subpopulations.

In British Columbia waters, available field evidence suggests that herring spawn at temperatures between 5 and 10 C in waters of reduced salinity. Stevenson (1962) concluded that salinities and temperatures of British Columbia spawning locations had no particular influence on survival of incubating eggs and larvae. He considered that year-class strength is probably related to the number of larvae that remain in inshore waters after hatching. Conversely, it was suggested that greatest, losses of young larvae could occur through their transport by adverse currents seaward into higher, less tolerable salinities, a conclusion indirectly supported by the current results.

In Table 5, laboratory estimates of salinity and temperature tolerance of Pacific herring eggs and larvae are compared with levels of those factors observed in association with natural spawning activities. The former provide ranges for salinity and temperature requirements of developing eggs and larvae (12–26‰ S, 5.5–8.7 C), which are in general agreement with field observations of salinities and temperatures associated with the latter (8–28‰ S, 3–9 C). Hence, the properties that have been studied in the laboratory appear to provide reasonable estimates of requirements under natural conditions.

In addition, salinity and temperature conditions found on the spawning grounds may be related to estimates of abundance of the Pacific herring over portions of its geographic range (Table 6). Unfortunately, measures of relative abundance are not available over most of the range, and observations of salinities and temperatures on spawning grounds are scarce and fragmentary. However, a comparison has been made as follows:

Abundance — approximated by comparing average annual landed catch of herring for particular areas of the North American coastline.

Spawning salinities — assumed not to be a limiting factor with respect to spawning grounds over most of the range. However, the availability of waters with both reduced salinity and appropriate temperature could be a limitation to spawning, particularly on the open coastline regions of American coastal waters.

Spawning temperatures — estimated from observations of sea surface temperature at various locations along the coastline, for the spawning period estimated for specific regions.

The landings of herring shown in Table 6 are not strictly comparable, as differences in fishing methods, fishing effort, and sizes of the fishing areas are not taken into consideration. For example, Alaska herring populations are not heavily exploited (Kasahara 1961) and are presumed to be larger than catch records would indicate. In addition, catches in the Monterey area are somewhat atypical, being taken largely by a summer fishery (main catch, April–October). The catch consists of adult and juvenile herring feeding in those waters but originating in large part in other statistical fishing areas (e.g., San Francisco area) (Miller and Schmidtke 1956). For a fishing period corresponding to the time of maximum herring catches in the San Francisco area, the average annual catch in the Monterey area (1948–67) would be not more than 10% of the figure shown in Table 6. The smaller figure would probably be a more representative estimate of a spawning population in the Monterey area. In addition, most of the Washington State herring catch is taken in the semi-enclosed and protected waters of Puget Sound, not from the open ocean coastline region.

The average temperature levels shown in Table 6 reflect the north–south ocean temperature gradient along the coast. They do not, however, indicate the extent of variation possible within the statistical areas, associated with freshwater inflow, weather, or local geography along the immediate coastline. For example, Miller and Schmidtke (1956) mention that, in San Francisco Bay and Tomales Bay (San Francisco area, Table 6), spawning in 1955 took place at temperatures between 8 and 10 C.

In the protected waters of the broken coastline regions of British Columbia, Washington (Puget Sound), and Alaska, waters of reduced salinity are common; in these areas the influence of salinity on spawning is difficult to define, considering the broad salinity range the herring egg will tolerate. However, observations near the southern limits of herring spawning appear to indicate the importance of salinity as one of the factors determining the location of spawning areas. Observations summarized by Miller and Schmidtke (1956) indicate that the location of spawning areas in the San Francisco Bay complex may be dependent on the extent of winter freshwater runoff into the Bay, and associated variation in the extent of saltwater intrusion into parts of the region. In general, the herring is said to spawn only in estuaries and bays in California waters, and not on the open coastline. Hence, south of British Columbia and the waters of Puget Sound, the more limited availability of large areas of reduced salinity would seem to restrict herring abundance through restriction of potential spawning salinities.

TABLE 5. Comparison of experimental data on salinity and temperature tolerance of Pacific herring eggs and larvae

Exptl observations	Salinity (‰)		Temp (C)		Reference
	Range	Optimum	Range	Optimum	
Fertilization	–	>5.0	–	–	Galkina 1957
Egg development					
Max strength of chorion	10–28	–	–	–	Galkina 1957
Total hatch (%)	–	12.01	–	6.46	This paper
Viable hatch (%)	10–24	16.98	6.5–10.5	8.33	"
Max larval size at hatching	–	20.00	–	5.54	"
Max size and % viable hatch	10–23	–	6.5–9.5	–	"
In min incubation time	13–19	16.98	7.6–8.7	8.7	"
Max salinity tolerance	11.53–16.24	–	–	–	McMynn & Hoar 1953
Rate of development independent of salinity	6.06–34.28	–	–	–	"
Larval tolerance	6.06–34.28	–	–	–	"
	10–42	22.6	–	–	Kurata 1959
	–	25.8	–	–	Fujita & Kobubo 1927
Jaw abnormalities, low temperature effect at	7.83–25.00	–	4.0–4.7	–	This paper
Hatched larvae most active, best developed	–	–	3–6	–	Nikitinskaya 1958
Longest survival on yolk supply	16.41–25.00	–	6.85–9.00	–	This paper
Total ranges	6–35	12–26	3–10.5	5.5–8.7	

The impression gained from the available evidence is that Pacific herring populations on the North American coast are confined to regions providing protected spawning waters of reduced salinity (8–28‰ S) at temperatures between about 5.0–5.5 C and 8.8 or 9 C, and that the size of these populations is related to the physical extent of the regions that provide these spawning requirements. The only significant area of spawning south of British Columbia and Puget Sound is that in San Francisco Bay. Its availability as a spawning area appears to be associated with the occurrence there of a reasonably large, protected body of water of reduced salinity at temperatures just within the upper spawning limit of about 10 C (see Table 5). Since herring spawnings in California are sporadic (Miller and Schmidtke 1956) in the smaller spawning areas, it is possible that minor annual water temperature fluctuations, probably also related to differences in freshwater runoff and its influence on areas of reduced salinity, could not only determine the success but also the occurrence of spawning in such areas.

In Japanese waters the southern boundary of spawning grounds is considered historically to be Toyama Bay, Honshu. Surface temperatures in Toyama Bay for the period of March to May, 1960–65 (Maritime Safety Agency, no date) ranged between 9.5 and 10.5 C. These records indicate that water temperatures in the spawning period near the southern boundaries of herring spawning are of the same order, namely 10 C, in both North American and Japanese waters.

Little evidence is available on the northern limits of spawning distribution in terms of temperature. However, the low/low–high/high interaction found between salinity and temperature with respect to percent viable hatch, suggests that spawning at high latitudes would probably be associated with coastal waters characterized by both low temperatures and low salinities.

with field observations associated with spawning. Ranges and optima shown for the current data are interpreted values.

Ecological observations	Salinity (‰) Range	Temp (C) Range	Optimum	Max	Reference
Approach & spawning					
Eastern Kamchatka	–	2.2–7	3–6	8	Svetovidov 1952
Peter the Great Bay	–	<0–?	4–9	–	"
Western South Sakhalin	–	<2–10	3–6	10	"
Western Sea of Okhotsk	–	0.5–10.7	–	–	"
Hokkaido	–	–	4–6	–	Motoda & Hirano 1961
Spawning conditions					
British Columbia	8.21–27.68	5.8–10.0	–	–	McMynn & Hoar 1953
"	–	–	7–8	–	Outram 1955
"	–	5–10?	–	–	Kasahara 1961
Kodiak	–	4–9?	–	–	"
NE Kamchatka	–	2.2–8	–	–	"
Penzhinsk	–	7–12	–	–	"
Okhotsk	–	3.5–10.0	–	–	"
Dekastri-Midwest Sakhalin	–	1.5–6.0	–	–	"
Hokkaido-S. Sakhalin	–	3–8	–	–	"
Peter the Great Bay	–	0.0–5.0	–	–	"
NE Korea	–	0.5–4.5	–	–	"
SE Korea	–	~10	–	–	"
General range	–	1–11	–	–	"
Japan Sea herring	17.43–18.47	–	–	–	Kurata 1959
Adults avoidance of high temp (spawning)	–	–	–	>10	Svetovidov 1952
Total ranges	8–28	<0–12	3–9	8–10	

On the basis of the tabulated evidence the following tentative conclusions are advanced:

- Pacific herring eggs and larvae are tolerant of a wide range of salinities (12–26‰ S) and herring generally spawn in those salinities (8–28‰ S), which optimize the measures of viability that have been investigated. On the basis of current laboratory evidence, maximum egg and larval survival is calculated to occur within a range of about 13–19‰ S, around an optimum at or near 16.98‰ S.
- Temperatures associated with optimum egg development (5.5–8.7 C) are contained within the temperature range in which most natural spawnings occur (3–9 C). On the basis of current results, maximum egg and larval survival is calculated to occur in British Columbia herring at or near a temperature of 8.7 C.
- Physiological differences may exist between British Columbia herring eggs and those of some Asian stocks, resulting in differences in low temperature tolerance. The latter apparently develop normally at and below temperatures that produce lower jaw abnormalities in British Columbia herring larvae (4.0–4.7 C).
- In North American waters, largest stocks of herring occur in those areas where spawning temperatures are about 5.0–5.5 C to 8.8 C or 9 C.
- Reduced spawning populations are associated with temperatures of 9–10 C toward the southern limits of North American distribution. In this region spawning appears to be limited to small estuarine and bay areas where both temperature and reduced salinity requirements can be met.
- The southern limit of spawning distribution in North American and Japanese waters coincides with water temperatures of about 10 C.

TABLE 6. Average annual catch of Pacific herring[a] from geographical areas of the North American coast in relation to estimated coastal sea surface temperatures[b] for the spawning periods shown.

Area	Avg annual landings, *lb*	Approx spawning period	Estimated coastal sea surface temp (*C*)	
			Mean min	Mean
South central Alaska	41970000	Apr.–June	2.3–6.2	5.5–7.5
Southeastern Alaska	66020000	Mar.–May	2.8–6.1	5.0–6.9
British Columbia	395773200	Feb.–Apr.	6.2–7.4	6.6–7.7
State of Washington	3357139	Feb.–Apr.	6.1–8.1	7.5–8.8
State of Oregon	–	–	–	11.1
State of California				
Eureka	25800	Dec.–Mar.[c]	8.1–8.8	10.0
San Francisco	1519613	Dec.–Mar.	9.0–10.1	10.9
Monterey	843040	Jan.–Feb.	10.8–11.0	11.9
Santa Barbara	18493	Jan.	11.1	12.0
Los Angeles	464	Jan.	12.8	13.8
San Diego	578	Dec.–Jan.	11.8–12.4	14.0

[a]South central Alaska and southeastern Alaska, 1941-58 (Kasahara 1961 table 16) British Columbia, 1948/49 to 1961/62 fishing seasons, exclusive of 1952/53 and 1957/58 (Taylor 1964 app. table 2); State of Washington, 1948–68 (Ward et al. 1968); State of California, 1948–67, for the statistical fishing areas indicated (California Department of Fish and Game 1951–68).

[b]Compiled as averages of monthly means for the spawning periods shown; locations selected, where possible, to reflect the influence of coastal conditions in the vicinity of known spawning grounds (from Coast and Geodetic Survey 1962; Hollister 1968).

[c]Assumed similar to San Francisco area.

In retrospect, further considerations of the effects of environmental factors on the spawning of Pacific herring, and survival of eggs and early larvae, would likely be assisted by the following: a more systematic collection of physical data on spawning times, and associated salinity and temperature levels, for representative stocks of Pacific herring over the range of the species; examination of salinity and temperature tolerance of eggs and larvae from representative stocks over the range; consideration of the relation that may exist between year-class strength and abnormally low (<5 C) or high (>10 C) spawning ground temperatures.

Acknowledgments

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Four Bomolochidae (Copepoda) from Fishes of British Columbia

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KABATA, Z. 1971. Four Bomolochidae (Copepoda) from fishes of British Columbia. J. Fish. Res. Bd. Canada 28: 1563–1572.

Holobomolochus venustus and *Holobomolochus occultus*, two new species of Bomolochidae (Copepoda: Cyclopoida) are recorded from fishes of British Columbia, described, and illustrated. *Holobomolochus spinulus* is found for the first time in the Canadian waters, and two new hosts (*Damalichthys vacca* and *Gasterosteus aculeatus*) are recorded for *Bomolochus cuneatus*.

KABATA, Z. 1971. Four Bomolochidae (Copepoda) from fishes of British Columbia. J. Fish. Res. Bd. Canada 28: 1563–1572.

L'auteur mentionne deux nouvelles espèces de Bomolochidae (Copepoda: Cyclopoida), *Holobomolochus venustus* et *Holobomolochus occultus*, parasites de poissons de la Colombie britannique. Il en donne une description accompagnée de dessins. Il rapporte pour la première fois la présence de *Holobomolochus spinulus* dans les eaux canadiennes et fait mention de deux hôtes nouveaux (*Damalichthys vacca* et *Gasterosteus aculeatus*) pour *Bomolochus cuneatus*.

Received January 7, 1971

REPORTS on the copepods parasitizing fishes in the waters of British Columbia include, so far, records of only one species belonging to the family Bomolochidae Claus 1875. This species, *Bomolochus cuneatus* Fraser 1920, has been found on the gills of several marine fishes along the coast of British Columbia, as well as in the Gulf of Alaska and off California (*Clupea harengus pallasi*, *Oncorhynchus gorbuscha*, *Leuresthes tenuis*, and *Cymatogaster aggregata*) (Vervoort 1964). The full extent of its host range is still unknown.

In the course of the last 2 years, some bomolochid copepods were found living on marine fishes off the coast of British Columbia. More bomolochid material was located in the fish parasite collection of Dr L. Margolis (Biological Station, Nanaimo B.C.). Upon examination, this material was found to comprise two new species of the genus *Holobomolochus* Vervoort 1969. Two additional previously known species were also present.

This paper reports on the results of the examination. It gives descriptions of the two new species and records of the two known ones. Standard examination methods were used. Berlese's fluid was employed as mountant and clearing agent, both for whole mounts and dissected appendages. Measurements of one new species (*Holobomolochus occultus*) were made under a dissection microscope. One specimen was measured in detail and total length of seven specimens was also measured (from the apex of rostral plate to the posterior tip of caudal rami, setae excluded). The specimens of the other new species (*Holobomolochus venustus*) had pronounced ventral flexion and could not be measured. Only one specimen was measured, under cover slip and with the aid of a compound microscope. Habitus drawings of this species, however, were made with the aid of a dissection microscope.

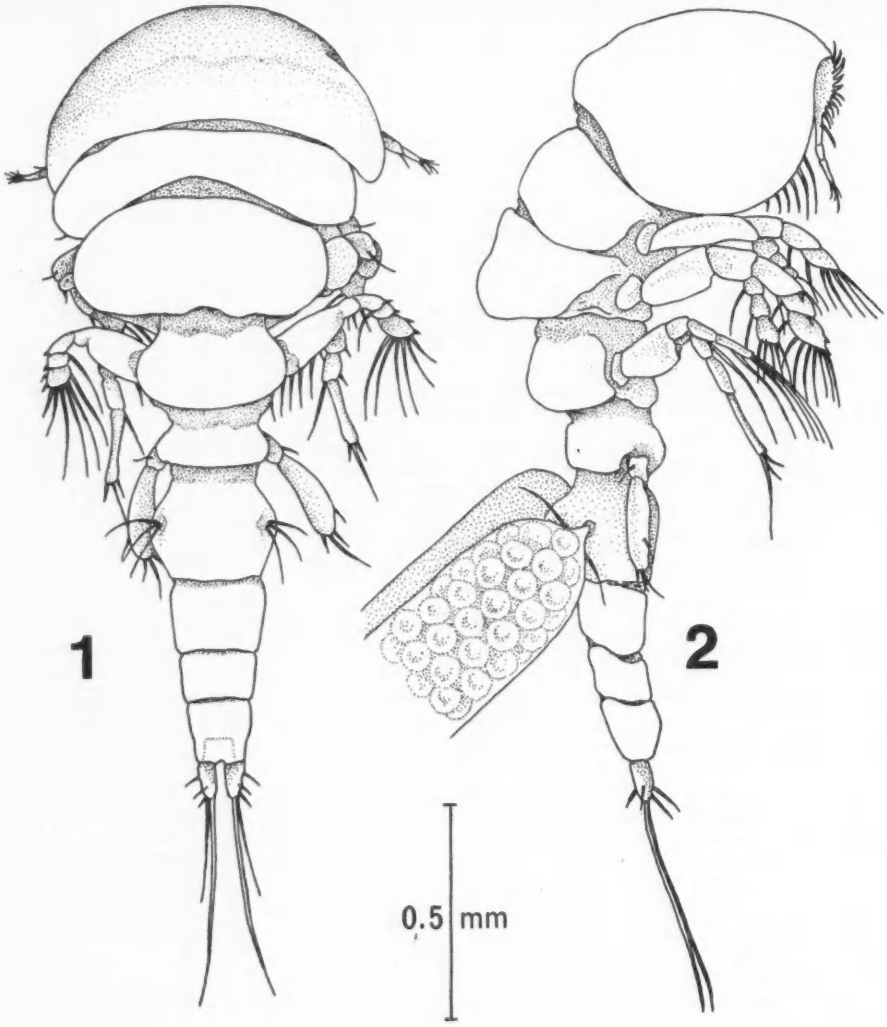
Holobomolochus venustus sp.nov.

Fig. 1–22

Record of specimens — (1) Many specimens, all female, were taken by Mr T. E. McDonald in Departure Bay, from the pier of the Biological Station in Nanaimo, B.C., on July 11, 1970; (2) five females were taken off Frederick Is., B.C., northern end of Queen Charlotte Islands, by Mr A. D. Sekerak. One female of the first lot becomes the holotype of the species and is deposited in the National Museum of Natural Sciences in Ottawa, Reg. No. NMC 15292. Four females of the same lot become paratypes and are stored in the same museum, Reg. No. NMC 15293.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

Printed in Canada (J2006)



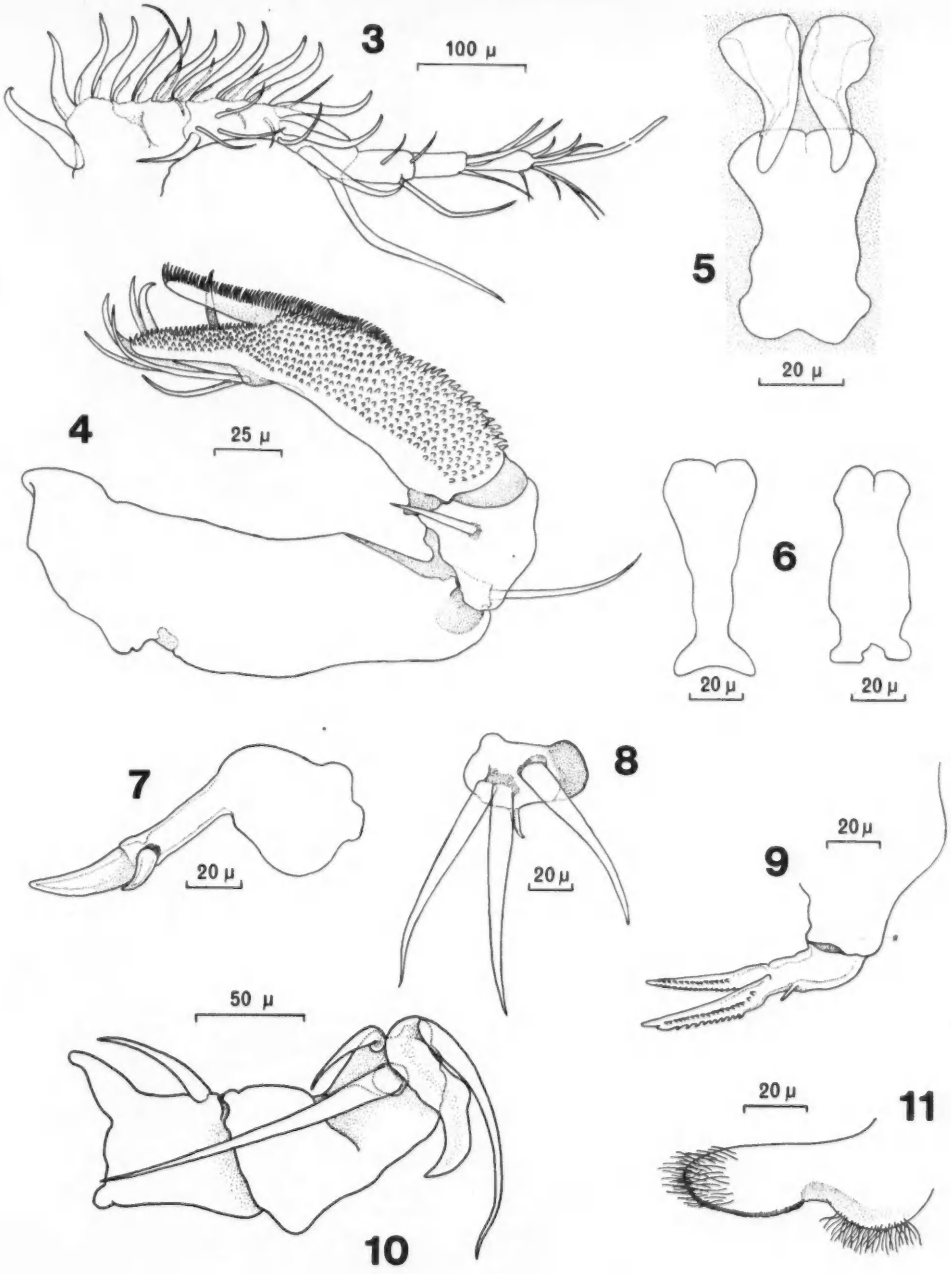
FIGURES 1–2. *Holobomolochus venustus*.
Fig. 1. Female, dorsal; Fig. 2. Same, lateral.

Hosts — (1) *Sebastodes caurinus* (Richardson 1844) (type host); (2) *Scorpaenichthys marmoratus* (Ayres 1854).

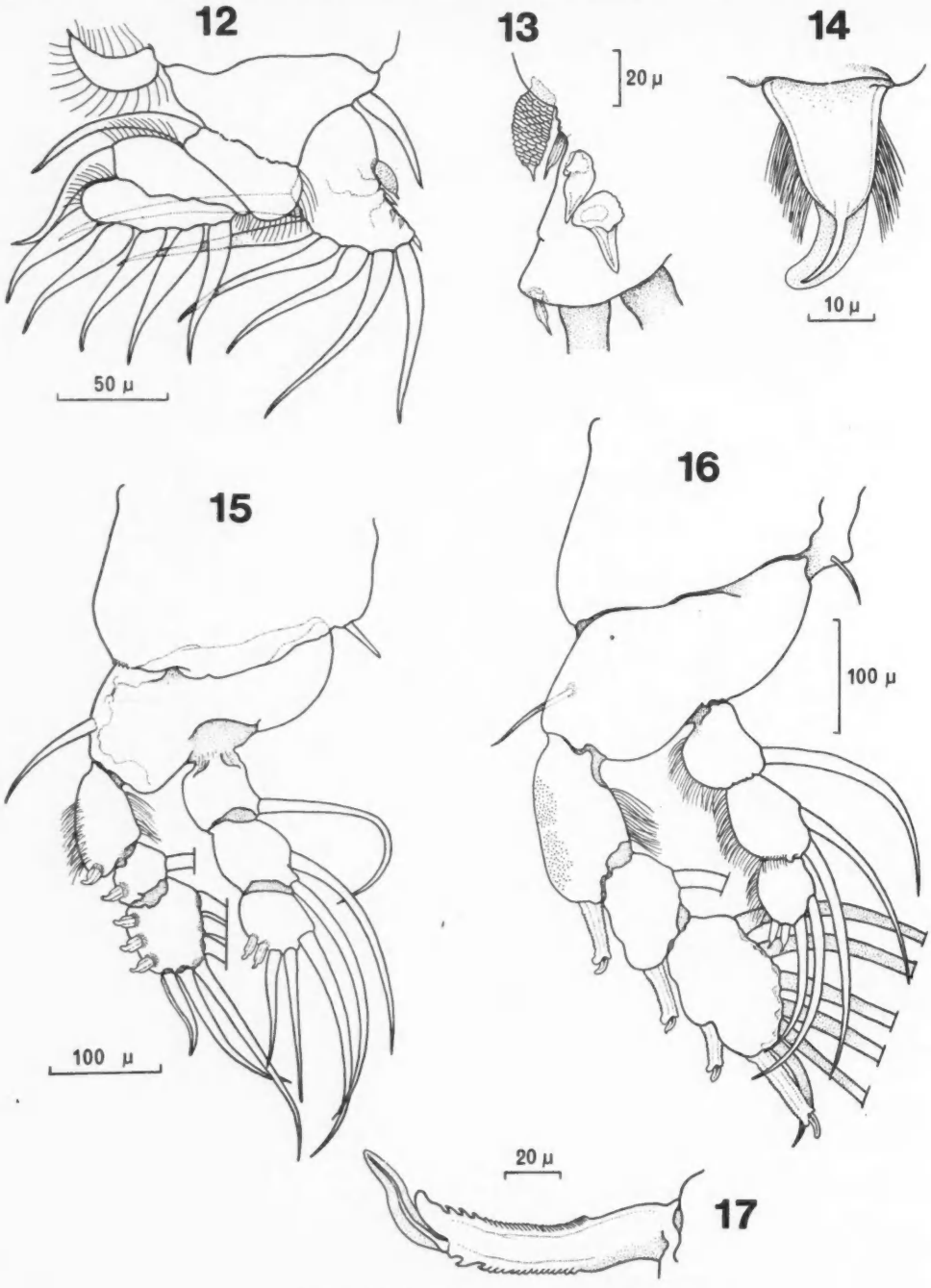
Habitat — Nasal cavity.

Female — Dimensions of specimen measured in detail: total length 2.03 mm; cephalic somite 0.622 × 0.940 mm, second thoracic somite 0.263 × 0.876 mm, third thoracic somite 0.190 × 0.678 mm, fourth thoracic somite 0.165 — 0.432 mm, fifth thoracic somite 0.190 × 0.267 mm; genital complex 0.254 × 0.262 mm; first abdominal somite 0.140 × 0.254 mm, second abdominal somite 0.114 × 0.203 mm; third abdominal somite 0.127 × 0.190 mm; caudal rami 0.102 × 0.063 mm (width at base). Longest furcal seta 0.630 mm. Egg sacs 0.920 × 0.260 mm.

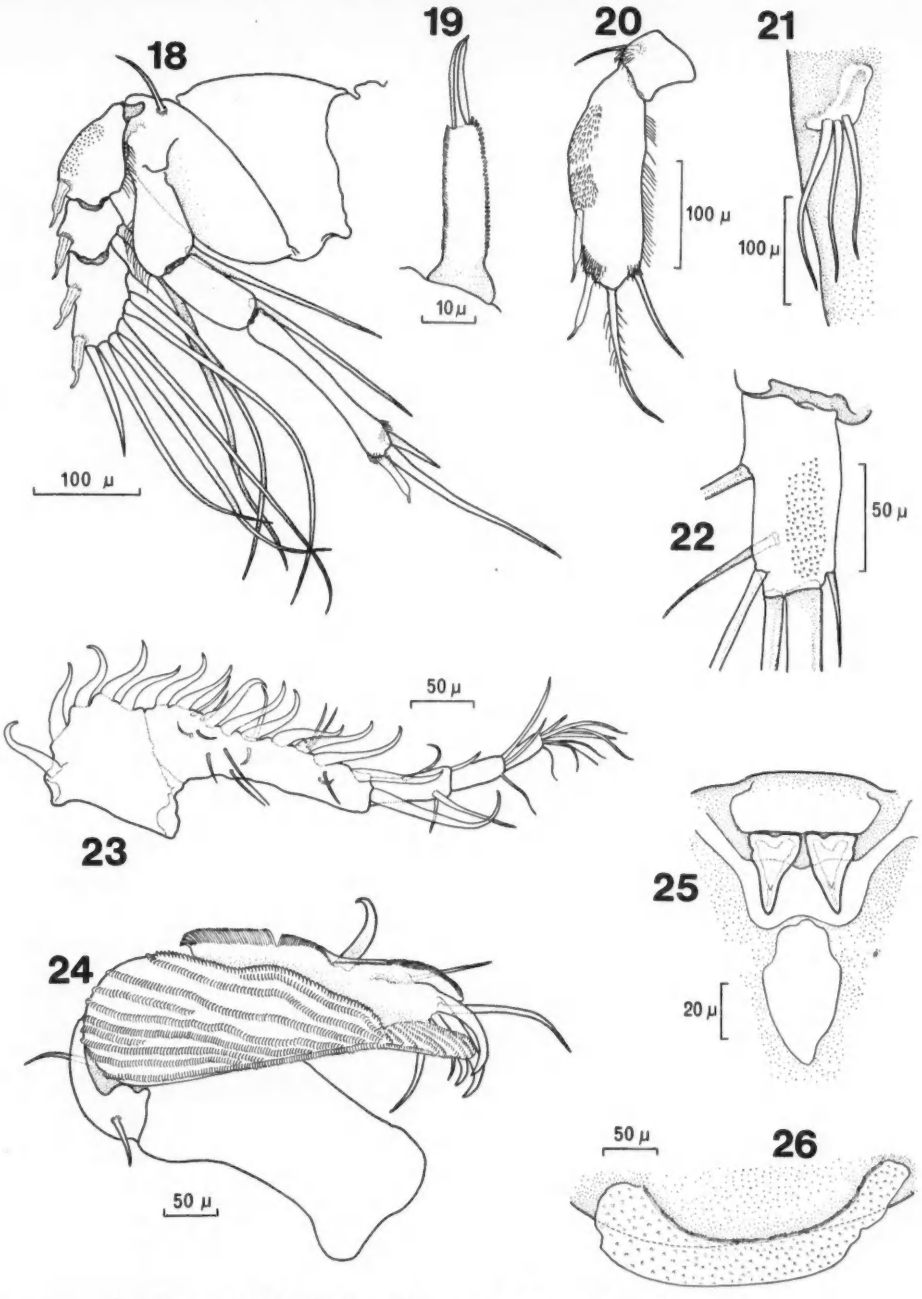
Cephalic somite flexed ventrally to longitudinal axis of body (Fig. 1, 2). Its lateral margins rounded, posterior margin transversely truncated. Lateral margins with marginal membrane, fine and transparent (usually



FIGURES 3–11. *Holobomolochus venustus*.
Fig. 3. First antenna, entire, ventral; Fig. 4. Second antenna, entire, ventral; Fig. 5. Rostral tines and subrostral plate, ventral; Fig. 6. Subrostral plates, ventral; Fig. 7. Mandible, dorsal; Fig. 8. First maxilla, ventral; Fig. 9. Second maxilla, ventral; Fig. 10. Maxilliped, ventral; Fig. 11. Paragnath, ventral.



FIGURES 12–17. *Holobomolochus venustus.*
Fig. 12. First leg, entire, ventral; Fig. 13. Same, exopod, detail of lateral margin; Fig. 14. Second leg, exopodal spine; Fig. 15. Second leg, entire, ventral; Fig. 16. Third leg, entire, ventral; Fig. 17. Same, exopodal spine.



FIGURES 18–26. *Holobomolochus venustus* and *Holobomolochus occultus*.
Fig. 18. *H. venustus*, fourth leg, entire, ventral; Fig. 19. Same, exopodal spine; Fig. 20. Fifth leg, ventral; Fig. 21. Sixth leg, dorsal; Fig. 22. Caudal ramus, ventral; Fig. 23. *H. occultus*, first antenna, entire, ventral; Fig. 24. Second antenna, entire, ventral; Fig. 25. Rostral tines and subrostral plate, ventral; Fig. 26. Lateral membrane of cephalic somite, ventral.

folded inward and difficult to see, not shown in Fig. 1, 2). Cephalic somite does not overlap following somite. Second thoracic somite narrow, with gently curving dorsal surface. Dorsal surface of third thoracic somite with humplike protrusion (Fig. 2). Fourth thoracic somite only two-thirds as wide as third somite (Fig. 1). Fifth thoracic somite only slightly narrower than fourth. Genital complex not very prominent (Fig. 2). Abdominal segments gradually narrow toward posterior extremity. Caudal rami slender, slightly tapering toward tips.

Rostral tines (Fig. 5) moderately long, with small protuberances on lateral margins about one-quarter length from tip.

First antenna (Fig. 3) of fused basal part and three well-defined distal segments. Main armature of basal part 15 robust, plumose setae (plumules omitted in figure), last seta much longer than remaining ones. All setae of similar structure, but setae 2–10 with small reinforcing plates along basal third. Ventral surface of basal part with one plumose seta and four slender, unarmed setae. Dorsal surface with five more similar setae. Slender seta at base of main seta 7 longer than main setae. First segment of distal part with three setae, second also with three setae and terminal segment with eight setae, one of them (aesthete?) much longer and thicker than others.

Second antenna (Fig. 4). Coxa constitutes about one-half of its length, long and robust, with one slender seta at junction with basis. The latter short, with one short, fairly strong seta. Endopod reflected toward base of appendage, with surface densely covered by small denticles arranged in poorly organized rows. Lamelliform process with row of fine, slender, relatively long denticles. Near fusion line of two endopod segments seven setae, four broad, sickle-shaped, other three less curved and weaker.

Upper lip covered by short, very fine setules, except for anterior margin and narrow strip in midventral line.

Mandible (Fig. 7) with rounded base and cylindrical masticatory process, with long, tapering tooth terminally and similar, smaller tooth subterminally, on dorsal side.

First maxilla (Fig. 8) small, subconical, with four setae; three large and the fourth much smaller. Second maxilla (Fig. 9) with robust base and two distal outgrowths. Ventral outgrowth with two rows of denticles on ventral and posteroventral surface. Dorsal outgrowth, in addition, with third row on dorsal surface (not seen in Fig. 9). Short, blunt seta near base of ventral outgrowth.

Paragnath (Fig. 11) of two parts, separated by notch in posterior margin. Proximal part rounded posteriorly, with fringe of setules. Distal part with finely serrated posterior margin and fringed apex.

Maxilliped (Fig. 10) lateral to other mouth parts. Coxa short, cylindrical, with a robust plumose seta about its own length. Basis long, with two plumose setae and claw. One seta very long, other shorter than claw. The latter flexed in mildly sigmoid curve, without auxillary denticle, with small swelling about midlength.

Armature formula for legs as follows:

Leg	Endopod	Exopod
1	1+0. 1+0. 5	6+V.
2	1+0. 2+0. 3+II.	0+I. 1+I. 5+IV.
3	1+0. 2+0. 2+II.	0+I. 1+I. 5+III.
4	1+0. 1+0. I+1+I.	0+I. 1+I. 6+II.

(Figures do not show plumules on large setae of legs.)

Leg 1 (Fig. 12) broad, short, considerably modified. Basal segment of sympod with broad, finely pointed lamella on medial margin. Lamella with dense fringe of setules. Exopod with obscure segmentation, fused. Proximal spine of lateral margin (Fig. 13) scaly and corrugated, with fine tip. Spines 2 and 5 short and simple, spines 3 and 4 robust, with broad bases.

Leg 2 (Fig. 15) with characteristic exopodal spines. Spines (Fig. 14) conical, with fringes of fine setules on sides of cone and tipped by whiplike process, flanged with membrane. Endopod spines of distal segment of similar structure. Distal segment of exopod with three such spines and one modified seta (numbered as spine in formula). One margin of seta with plumules arranged as half of pinna, other with narrow strip of membrane. Exopod and endopod segments of about same width and size.

Leg 3 (Fig. 16). Proximal segment of exopod with batches of small tubercles on dorsal surface (ghosted in Fig. 16). Exopod spines (Fig. 17) long, cylindrical, with two rows of serrations along most of its length and with subterminal whiplike outgrowth, rimmed with membrane. Exopod much more massive than endopod.

Leg 4 (Fig. 18) with modified endopod. The latter with greatly elongated distal segment. Exopodal spine (Fig. 19) smaller and more finely armed than that of leg 3. Proximal segment of exopod with dorsal batch of small tubercles.

Leg 5 (Fig. 20) two-segmented. Basal segment short, subquadrangular; distal longer, somewhat spatulate. Proximal segment with batch of setules in lateral corner and longer, slender seta on dorsal surface. Distal segment with fine setules on ventral surface (arranged in three batches), fringe of setules on medial margin and batch of setules at base of medial naked seta. Laterodistal corner with spine and distal margin with long, pinnate seta.

Leg 6 (Fig. 21) consists of three long, pinnate setae, on dorsal side of genital complex.

Caudal ramus (Fig. 22) with batch of denticles on ventral surface. Armature of six setae. Terminal margin with two setae, longest and stoutest medial, second longest lateral. One smaller seta in distolateral and one in distomedial corner. Fifth seta on lateral margin and sixth on dorsal surface.

Male — Unknown.

Holobomolochus occultus sp.nov.
Fig. 26–38

Record of specimens — (1) Many ovigerous females were taken off the west coast of Vancouver Island during a cruise of *G.B. Reed*, June 1968; (2) four ovigerous

females were taken in Chatham Sound (border of British Columbia and Alaska), on January 28, 1954. One female of the first lot becomes the holotype of the species and is preserved in the National Museum of Natural Sciences in Ottawa, Reg. No. NMC 15290. Sixteen females become paratypes and are kept in the same museum, Reg. No. NMC 15291.

Hosts — (1) *Lyopsetta exilis* (Jordan and Gilbert 1880) (type host); (2) *Hippoglossoides elassodon* Jordan and Gilbert 1880.

Habitat — Gills and gill cavity.

Female — Total length from 1.39 to 1.92 mm. Cephalic somite 0.508 × 0.894 mm, second thoracic somite 0.127 × 0.834 mm, third thoracic somite 0.179 ×0.597 mm, fourth thoracic somite 0.127 × 0.241 mm, fifth thoracic somite 0.089 × 0.236 mm; genital complex 0.165 × 0.241 mm; first abdominal somite 0.076 × 0.165 mm, second abdominal somite 0.063 × 0.140 mm, third abdominal somite 0.063 × 0.114 mm; caudal rami 0.051 × 0.038 mm (width at base). Longest furcal seta 0.394 mm. Egg sacs 1.079 × 0.240 mm.

Cephalic somite semicircular in dorsal aspect. Lateral membranes prominent and easy to see (Fig. 26–28). Anterior margin of cephalic somite with central protrusion. Ventral flexion of cephalic somite gentle and gradual (Fig. 28). Dorsal surfaces of thoracic somites 2–5 smooth and without projections. Fourth somite much narrower than third (Fig. 27) and partly overlapped by it. Genital complex subcircular. Abdomen relatively short and squat. Caudal rami shorter and broader than in preceding species.

Rostral tines (Fig. 25) short and pointed.

First antenna (Fig. 23) with structure similar to that of *H. venustus*. Basal part with five setae on ventral surface, five on dorsal and four on anterior, just dorsal to the row of main 15 plumose setae. Distal part armed as in *H. venustus*, but apical armature without one dominant seta (aesthete?).

Second antenna (Fig. 24) shorter and stouter than in *H. venustus*. Coxal segment robust and armed distally with one slender seta. Basis short and also with one seta. Surface of endopod with oblique rows of scaly denticles. Some rows shorter than others. Lamelliform process with row of fine denticles. Seven setae near point of fusion of two endopod segments, three sabrelike, and four more slender and less curved. Another sabrelike seta at some distance toward the base of the ramus from others.

Upper lip with patches of fine setules in posterolateral corners.

Mandible resembles that of *H. venustus*.

First maxilla (Fig. 29) small, conical, with four setae: two small and two prominent with rows of setules along entire lengths. Second maxilla (Fig. 30) with two terminal outgrowths, apparently devoid of any armature except for a toothlike projection in subterminal position. Tips rounded. Styletlike seta near the base of the outgrowths.

Details of paragnath structure were not established.

Maxilliped (Fig. 31). Coxal segment fairly long, robust, with medium long, strong, plumose seta. Basis long, slightly curving anteriorly, with conical swelling posteriorly. Two short plumose setae on concave margin. Segment distally articulates with claw. At base of claw, narrow, corrugated adhesion pad. Claw curved in sigmoid fashion, with secondary tooth on convex margin at point of distal curve. Prominent plumose seta arises from claw, near its base.

Leg armature formula as follows:

Leg	Endopod	Exopod
1	1+0. 1+0. 5+I.	6+V.
2	1+0. 2+0. 3+II.	0+I. 1+I. 5+IV.
3	1+0. 2+0. 2+II.	0+I. 1+I. 5+III.
4	1+0. 1+0. I+1+I.	0+I. 1+I. 5+III.

All segments of leg 1 broad and short (Fig. 33). Endopod distinctly segmented and much longer than exopod. Latter almost completely fused. Five lateral spines of exopod (Fig. 34) similar to one another, differing mainly in length. Basal segment of sympod with short fringe of setules laterally. Similar fringe on lateral margins of all endopod segments.

Leg. 2 (Fig. 36) with endopod larger than exopod. Fringe of setules on lateral margin of proximal segment of sympod. Distal segment with slender plumose seta on dorsal surface, near lateral margin. Exopodal spines of all legs similar (Fig. 32), with broad flanges on two sides and terminal outgrowth.

Leg 3 differs from leg 2 only in armature formula.

Leg 4 (Fig. 37) similar to preceding pairs but with relatively smaller endopod. Segments of endopod not elongated.

Leg 5 (Fig. 38) short and squat, of two segments. Basal segment almost quadrangular with slender seta on dorsal surface and laterally with short fringe of bristlelike setules. Distal segment oblong, bearing terminal plumose seta and subterminal three spines, similar to those of preceding legs. Fringes of setules near bases of all spines and seta.

Leg 6 as in *H. venustus*.

Caudal ramus (Fig. 35) has no denticulation on its broad surfaces. A row of denticles present on ventral margin of the last abdominal segment along junction with caudal ramus and curving in anterior direction. Two terminal long setae of about same thickness at base, but of different lengths.

Male — Unknown.

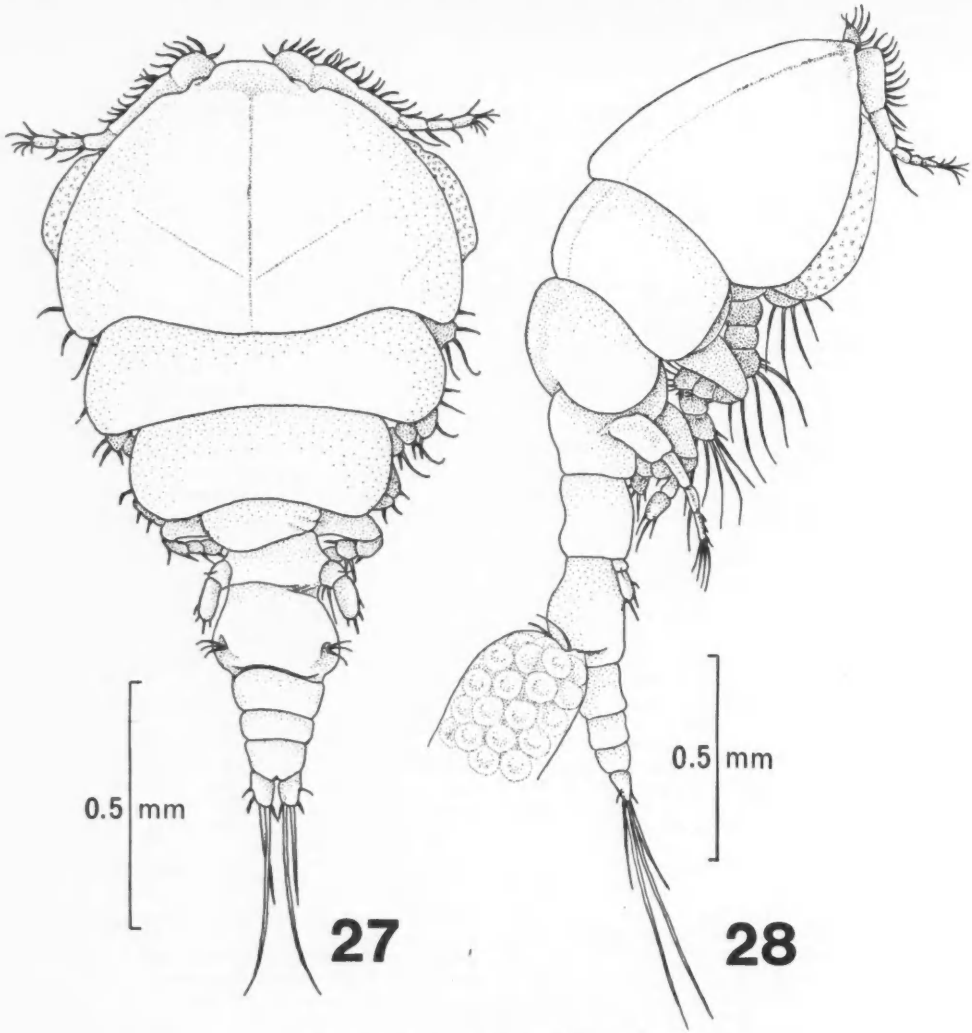
Holobomolochus spinulus (Cressey 1969) n.comb.

Syn. *Bomolochus spinulus* Cressey 1969

Record of specimens — Several female specimens were found in the collection of Dr L. Margolis. They were taken in Departure Bay, off Nanaimo, east coast of Vancouver Island B.C., on September 15, 1953.

Hosts — *Oligocottus maculosus* Girard 1856; *Leptocottus armatus* Girard 1854.

Habitat — Gills.



FIGURES 27–28. *Holobomolochus occultus.*
Fig. 27, Female, dorsal; Fig. 28. Same, lateral.

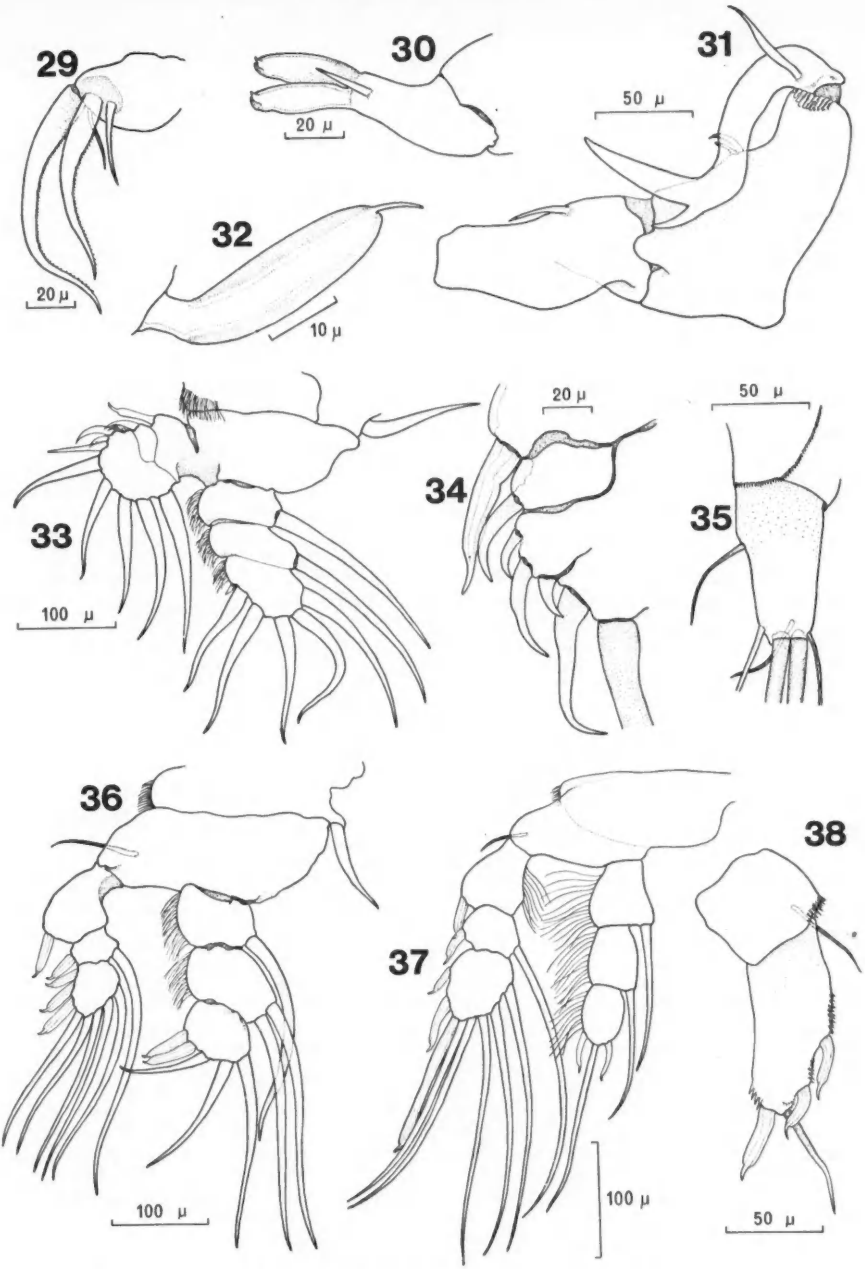
Previous record — Cressey (1969) described this species from *Scorpaena guttata*, *Oxylebius pictus*, *Sebastodes mystinus*, and *S. serranoides*, all from La Jolla, California. The description was produced before the revision of the genus *Bomolochus* was published by Vervoort (1969), hence the species was placed in this genus. On the basis of the new diagnosis of *Bomolochus* and related genera, it clearly belongs to the genus *Holobomolochus*, as shown by the structure of its first antenna. (The same applies to *Bomolochus longicaudus* and *B. prolixus*, described by Cressey in the same publication.)

H. spinulus is new to the Canadian fauna and its find also constitutes two new host records.

Bomolochus cuneatus Fraser 1920

Syn. *Parabomolochus cuneatus* (Fraser 1920)

Record of specimens — Two lots of female specimens were located in the collection of Dr L. Margolis. One had been taken in Departure Bay, off Nanaimo, on September 15, 1953, the other had come from Windsor Cove, Burke Channel, B.C., in June 1963.



FIGURES 29–38. *Holobomolochus occultus.*
Fig. 29. First maxilla, ventral; Fig. 30. Second maxilla, ventral; Fig. 31. Maxilliped, ventral; Fig. 32. Exopodal spine of legs two to five; Fig. 33. First leg, entire, ventral; Fig. 34. Same, exopod, detail of lateral margin, ventral; Fig. 35. Caudal ramus, ventral; Fig. 36. Second leg, ventral; Fig. 37. Fourth leg, ventral; Fig. 38. Fifth leg, ventral.

Hosts — (1) *Damalichthys vacca* Girard, 1885; (2) *Gasterosteus aculeatus* L.

Previous records of this parasite in waters of British Columbia were mentioned in the introduction. This find constitutes two new host records.

Discussion

The armature of the first four pairs of legs is sufficient to differentiate between the two newly described species, *H. venustus* and *H. occultus*. It also suffices to distinguish both of them from the previously known species of the genus *Holobomolochus*. *Holobomolochus venustus* differs from *H. occultus* in the armature of the exopod of the first leg. From *Holobomolochus nothrus* (Wilson) it differs in the exopod of the first leg; from *Holobomolochus ardeolae* (Krøyer) in both rami of the first leg, exopod of the second, both rami of the third, and the exopod of the fourth leg; from *Holobomolochus attenuatus* (Wilson) in the exopods of legs one to four; from *Holobomolochus palleucus* (Wilson) and *Holobomolochus albidus* (Wilson) in the exopod of the first leg; from *Holobomolochus acutus* (Gnanamuthu) in the exopod of the first and fourth leg and both rami of the second; from *Holobomolochus confusus* (Stock) in both rami of the first leg; from *Holobomolochus prolixus* (Cressey), *Holobomolochus spinulus* (Cressey), and *Holobomolochus longicaudus* (Cressey) in the exopod of the first leg.

Holobomolochus occultus differs from *H. nothrus* in the structure of the exopod of the first leg; from *H. ardeolae* in both rami of the first and the third leg and the exopod of the second and the fourth leg; from *H. attenuatus* in both rami of the first leg and the exopod of the second, third, and fourth legs; from *H. palleucus*, *H. albidus*, *H. confusus*, *H. prolixus*, and *H. longicaudus* in both rami of the first leg and from *H. acutus* in both rami of the first and second leg and the exopod of the fourth.

Some differences between other appendages of the two new species and some of the previously known ones have also been found, but not all species of *Holobomolochus* have been studied in sufficient detail to make comparison of these appendages of more than questionable value. At any rate, the differences enumerated above are sufficient to justify the recognition of these two species as valid taxa.

In describing the two new species of *Holobomolochus*, I observed in their rostral area a structure hitherto never reported in the literature. This structure, a small sclerite, situated on the ventral side within the reach of the rostral tines, I refer to as the subrostral plate. It is illustrated in Fig. 5, 6, and 25. The shape of the subrostral plate differs fairly widely from one specimen to another within the same species (compare Fig. 5 and 6) but these differences are much smaller than those between the subrostral plates of different species (compare Fig. 5 and 6 with Fig. 25). Having looked at six species of bomolochids, I believe that this structure merits further attention as a possible diagnostic feature of these copepods.

Acknowledgments

I am grateful to Dr L. Margolis, Biological Station, Nanaimo, for placing at my disposal his collection of bomolochid copepods used in this work.

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Relation Between Production and Biomass

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ALLEN, K. R. 1971. Relation between production and biomass. J. Fish. Res. Bd. Canada 28: 1573–1581.

A series of mathematical models of cohorts in animal populations representing various combinations of several different simple growth and mortality functions is examined to investigate the ratio between mean biomass and production over unit time, and to compare this ratio with the mean age and mean life span of the animals in the cohort.

For any cohort, the ratio of production per unit time to mean biomass is equal to the ratio of total production by the cohort to its total biomass integral by time. For populations consisting of a number of simultaneous, successive, or overlapping cohorts, the ratio of production per unit time to mean biomass is equal to the mean of the ratios for the individual cohorts weighted by the mean biomasses of the cohorts.

If the cohorts are identical, the population ratio is the same as the cohort ratio and problems arising from the presence of more than one cohort may be ignored. Formulations for the total production per cohort, biomass integral, and, where they can be simplified, their ratios, are given.

Comparison with mean age and mean life span shows that for constant exponential mortality, mean age and mean life span are both equal to the reciprocal of the production–biomass ratio. For other mortality functions, if growth in weight is linear, the production–biomass ratio equals the reciprocal of the mean age. For other models there is no simple relation. In general, mean age appears a better approximation than mean life span to the reciprocal of the production–biomass ratio.

These methods are applied, as an example, to Antarctic krill, using a model having linear growth in length and four periods with different exponential mortality rates. For this model, annual production is 1.8 times the mean biomass so that assumption of equality leads to an underestimate of production. Mean age and mean life span are 0.21 and 0.037 years respectively. Thus, use of either of these as an approximation, and particularly mean life span, leads to severe overestimation of annual production.

ALLEN, K. R. 1971. Relation between production and biomass. J. Fish. Res. Bd. Canada 28: 1573–1581.

Ce travail présente une série de modèles mathématiques de cohortes au sein de populations d'animaux offrant divers combinaisons de plusieurs différentes fonctions simples de croissance et de mortalité. On y examine le rapport de la biomasse moyenne à la production par unité de temps, et on compare ce rapport à la moyenne d'âge et à la durée moyenne de la vie des membres de la cohorte.

Pour une cohorte donnée, le rapport production par unité de temps/biomasse moyenne est égal au rapport production totale/intégrale temporelle de biomasse. Dans le cas de populations formées de plusieurs cohortes simultanées, successives ou chevauchantes, le rapport production par unité de temps/biomasse moyenne égale la moyenne des rapports de chaque cohorte équilibrée par la biomasse moyenne des cohortes.

Dans le cas de cohortes identiques, le rapport de la population est semblable à celui de la cohorte et on peut ne pas tenir compte des problèmes inhérents à la présence de plus d'une cohorte. Nous montrons les formules de production totale par cohorte, l'intégrale de biomasse et, là où ils peuvent être simplifiés, les rapports qui existent entre les deux.

En comparant la moyenne d'âge à la durée moyenne de la vie on se rend compte que, pour une mortalité exponentielle constante, ces valeurs sont toutes deux identiques à l'inverse

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This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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du rapport production/biomasse. Quant aux autres fonctions de mortalité, si la croissance en poids est rectiligne, le rapport production/biomasse est égal à l'inverse de la moyenne d'âge. Il n'y a pas de relation simple pour les autres modèles. En général, la moyenne d'âge est une meilleure approximation que la durée moyenne de la vie pour le calcul de l'inverse du rapport production/biomasse.

A titre d'exemple, nous avons appliqué ces méthodes au krill antarctique. Nous avons utilisé un modèle doté d'une croissance en longueur rectiligne et de quatre périodes à taux de mortalité différentielle différents. Dans ce modèle, la production annuelle est 1.8 fois plus grande que la biomasse moyenne, de sorte que l'hypothèse que ces valeurs sont égales conduit à une sous-évaluation de la production. La moyenne d'âge et la durée moyenne de la vie sont de 0.21 et 0.037 ans respectivement. On risque donc une sérieuse surestimation de la production annuelle si on emploie comme approximation l'une ou l'autre de ces valeurs, surtout celle de la durée moyenne de la vie.

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PRODUCTION, here defined as the total amount of tissue elaborated in the population or community under study during a given period, is a dynamic quantity that can rarely be measured directly. Its measurement or estimation calls essentially for knowledge of the biomass of the population or community at the beginning and end of the period and of the mass of living components that have been lost by death or emigration during the period. Except under closely controlled experimental conditions, the last quantity can rarely be directly observed with any useful degree of accuracy. Estimation of production, therefore, calls for indirect methods and those so far developed seem to fall into three principal categories: those in which production is estimated from knowledge of the number and size of the individuals in the population at a series of points in time; those based on estimates of the amount of food consumed by the population and the efficiency of its conversion into the tissues of the population components; and those based on estimates of the food consumption of a predator population, which is assumed to take up most of the production to be estimated. This paper is concerned with certain aspects of the first type of approach. Essentially, all the methods in this category involve the application of some mathematical technique to the basic data of number and individual mass. Thus, the method of Ricker (1946) involves first using the individual mass data to determine the instantaneous growth rate (G) and then computing the production by the formula $P = G\bar{B}$, where $\bar{B}$ is the average biomass during each period. If it can be assumed that during the period the instantaneous mortality rate (Z) is also constant and known, production can be calculated from a single observation on biomass by the formula

$$P = \frac{GB(e^{G-Z} - 1)}{G - Z}.$$

In nature, Z and particularly G rarely remain constant during the life span of an animal. In such cases this technique can still be applied to a succession of subperiods within which it can reasonably be assumed that both G and Z are constant. It may, however, be more satisfactory and less laborious to use a formula for calculating production based on a growth curve that more closely resembles those found in nature and thus avoid the subdivisions of the life span that are otherwise required. Formulae suitable for this approach have been developed for the negative exponential growth curve by Allen (1950) and for the von Bertalanffy growth curve by Gulland in Chapman (1968).

The graphical method of estimating production (Allen 1951) is, of course, the solution by mechanical means of the equation

$$P = \int_{W_1}^{W_2} N_t dW_t = \int_{T_1}^{T_2} N_t \frac{dW_t}{dt}\, dt,$$

where N_t and W_t are the number of animals and, the mean individual weight respectively at time t.

Attempts have also been made, when less detailed data have been available, to obtain useful approximations to production over a given period by applying a suitable multiplier directly to the mean biomass over the period. It was early suggested (Lindeman 1941) that an estimate of annual production could be obtained by multiplying mean biomass by the number of "turnovers" in the year, and Lindeman appears to have regarded turnovers as equivalent to life cycles or generations. This, however, must lead to an underestimate of total annual production (Allen 1951). More recently, McArthur, in Leigh (1965), has stated that the ratio of production to biomass is the appropriately weighted harmonic mean of the life spans of the species in a community. This is, however, only true within certain conditions of growth and mortality.

Waters (1969) has taken a reverse approach and defined turnover ratio (TR) as the ratio of production over a defined period to mean biomass. He has then determined this ratio for a number of

freshwater benthic invertebrates, taking the life of one cohort as the time interval, and compared the results with those obtained for various empirical curves relating number and individual size in the cohort. He has found that TR is commonly between 2 and 5.

The purpose of the present paper is to examine, in more detail, the nature of the ratio between production and mean biomass, and to express it mathematically for several models for mortality and growth.

Production by a Single Cohort

As a first step, production and biomass may be considered within a single cohort of animals all born at one time. If T is a period of time long enough for all these animals to have died, then the total production (P) by the cohort and its mean biomass ($\bar{B}$) during the whole period T are given by

$$P = \int_0^T \frac{N_t \, dW_t}{dt} \, dt$$

and

$$\bar{B} = \frac{1}{T} \int_0^T N_t W_t dt.$$

Then, if B^* is the biomass integral by time, i.e.,

$$B^* = \int_0^T N_t W_t dt$$

and R is the ratio of production per unit time (P') to mean biomass, we have

$$R = \frac{P'}{\bar{B}} = \frac{P/T}{B^*/T} = \frac{P}{B^*}.$$

Thus, for any cohort, we have the basic theorem that the ratio of production per unit time to mean biomass is equal to the ratio of total production by the cohort to its total biomass integral by time.

Production by Additional Cohorts

This theorem may be extended to cases in which a number of cohorts exist simultaneously or in succession in a single population. If, within time T, N cohorts pass through their cycle, then, whether or not they overlap in time, total production and total mean biomass are given by

$$P = \sum_{n=1}^{N} P_n$$

and

$$\bar{B} = \frac{1}{T} \sum_{n=1}^{N} B_n^*$$

so that, for the whole population

$$R = \frac{\frac{1}{T}\sum_{n=1}^{N} P_n}{\frac{1}{T}\sum_{n=1}^{N} B_n^*} = \frac{\sum_{n=1}^{N} R_n B_n^*}{\sum_{n=1}^{N} B_n^*}.$$

Thus, the population ratio of production per unit time to mean biomass is equal to the mean of the ratios for the individual cohorts weighted by the biomass integrals or by the mean biomasses of the cohorts. In cases where the cohorts are identical in their growth and mortality, then the ratio for the whole population is the same as that for any one cohort, and it is therefore unnecessary to consider effects due to the existence of more than one cohort during the period under study.

The same reasoning may, of course, be applied to a community consisting of any number of species. It is immaterial whether the cohorts are of the same species or not. However, in this case the production calculated is the gross production of the community in which the same materials may be included more than once if several trophic levels are involved.

Production : Biomass for Model Cohorts

Application of this theorem makes it relatively simple to calculate the ratio of production per unit time to mean biomass for any population for which a satisfactory mathematical model of growth and mortality can be constructed, provided that the production and biomass integrals can be formulated in mathematical terms. In the present study the formula expressing the ratio has been determined for a number of models incorporating various mortality and growth curves.

The mortality models examined have been:

(*a*) *Simple exponential mortality*, i.e.,

$$N_t = N_0 e^{-Zt};$$

(*b*) *Multiple exponential mortality*, in which the life span is divided into N intervals, such that in the nth interval, T_{n-1} to T_n, the instantaneous mortality rate is Z_n, so that

$$N_t = N_0 e^{-\left[Z_n(t-T_{n-1}) + \sum_{i=1}^{n-1} Z_i(T_i - T_{i-1})\right]};$$

(*c*) *Linear models*, in which deaths occur at an absolute constant rate until the last animal dies after time T, i.e.,

$$N_t = N_0\left(1 - \frac{t}{T}\right);$$

(*d*) *Fixed life span* so that all animals survive until time T and then all die simultaneously.

The growth models used are

(1) *Exponential growth* at a constant instantaneous rate, i.e.,

$$W_t = W_0 e^{Gt};$$

(2) *Simple asymptotic growth*, following a negative exponential model and assuming that weight is zero at zero time, i.e.,

$$W_t = W_\infty(1-e^{-Kt});$$

(3) *von Bertalanffy growth*, assuming isometric growth and that weight is zero at zero time, i.e.,

$$W_t = W_\infty(1-e^{-Kt})^3;$$

(4) *Linear growth in length*, assuming isometric growth, and that after time T weight is W_T, i.e.,

$$W_t = \frac{W_T\, t^3}{T^3};$$

(5) *Linear growth in weight*, such that weight is W_T after time T, i.e.,

$$W_t = \frac{W_T\, t}{T};$$

(6) *Growth proportional to* t^m. The two preceding models are special cases of this.

$$W_t = W_T\left(\frac{t}{T}\right)^m.$$

Table 1 shows the formulae for the production and biomass integrals for the population models derived by all combinations of these mortality and growth models. It also shows the ratio between them where this contains a useful amount of simplification. The asterisk (*) in the ratio column signifies that no useful simplification from the ratio of the two original integrals has been found. In the expressions for the integrals the following additional symbols have been used to produce some simplification: D_n = proportion of original population dying during the *n*th period; S_n = proportion of original population surviving at end of *n*th period; W_n = individual weight at end of *n*th period; B_n = biomass at end of *n*th period.

P/B Ratio, Age, and Life Span

In Table 2 these ratios are summarized for the various growth and mortality models. Where the ratios are complex they are expressed as functions of the variables concerned. Two interesting generalizations may be noticed in this table. The first is that with constant exponential growth the ratio is equal to the instantaneous growth rate, whatever the mortality model may be. The second is that, for any other growth model, the ratio for exponential mortality at a constant instantaneous rate is equal to the instantaneous mortality rate. For all the other models the ratio is a more complex function of the growth rate or mortality rate, or both. For growth proportional to t^m, including the linear models, the parameter T is itself a component of one or both of these rates.

Table 2 also shows for each of the mortality models the mean life span (i.e., mean age at death, $\frac{1}{N_0}\int t\frac{dN}{dt}dt$), and the mean age ($\int tN_t dt \Big/ \int N_t dt$) over the whole life of the cohort. For exponential mortality at a constant rate, mean age and mean life span are, of course, equal and, except when growth is exponential, both are equal to the reciprocal of the production–biomass ratio. In all the other cases in which growth in weight is linear, the production–biomass ratio is equal to the reciprocal of the mean age. In the remaining combinations the ratio has no fixed simple relation to either mean age or mean life span.

It is evident, therefore, that to obtain an estimate of the production–biomass ratio for use in estimating production, it is necessary to have as much information as possible regarding the nature of both growth and mortality curves. In the absence of this information, the reciprocal of mean age may be a more generally useful approximation than that of mean life span, since, when growth in weight is linear, it is directly applicable for several different types of mortality models. When growth in length is linear, mean age appears to lead to an underestimate of the ratio, and therefore of production, although the error is less than that using mean life span.

Application to Antarctic Krill

As an example of the application of these techniques, the estimation of production in Antarctic krill (*Euphausia superba*) may be considered. Gulland (1970) has taken the total standing crop of krill in the Antarctic to be 75 million tons, although Hempel (1970) points out that this estimate is somewhat too low due to confusion between dry and wet weights. He has then assumed that the mean life span is 1 year and that, consequently, annual production is equal to mean biomass. He has thus obtained an estimate of 75 million tons for annual production.

Although the available data regarding the growth and mortality of euphausiids are limited, they are probably sufficient to provide a better approximation to the production–biomass ratio than an assumed value of 1.0.

Marr (1962) has published extensive data regarding the mean size of samples of *E. superba* in the Antarctic at various ages. These data are arrayed in his fig. 55, and it is apparent that, ignoring some seasonal fluctuations in growth rate, an overall model of linear growth in length is a reasonably good fit to the data.

The data regarding mortality in this species appear to be very much less adequate but a comprehensive account has been given for another euphausiid, *Meganyctiphanes norvegica*, by Mauchline and Fisher (1969). Summarizing their statements, it appears that the numbers decrease quite rapidly from the egg to the early larval stages (calyptopes) (from 200–400 to 10–100 per m^3), but that mortality is less rapid through the later larval stages (furciliae) and up to the first breeding season at 1 year old. From the first to the second breeding seasons, mortality is comparatively small, the relative numbers of 0-group and 1-group animals being given as 1:1 to 2:1 for March and 3:1 to 4:1 for April. Taking an approximate average of these figures gives an estimate of 50% survival from the first to the second breeding seasons. This estimate is consistent with the statement of Ponomareva (1963) for another species of euphausiid (*Thysanoessa inermis*) that "losses among the one-year-olds amount to 40-50%." In *Meganyctiphanes* the mortality rate apparently increases again after the second breeding season, and Mauchline and Fisher (1969) state that only about 5–10% of the breeding 2-year-olds survive to breed for a third time. Further data regarding early mortality can be deduced by using the number of eggs per breeding female. This is given by Mauchline and Fisher (1969) as 530 for *Meganyctiphanes* and as 310–800, depending upon size, for *E. superba*. A useful approximate figure, therefore, appears to be 500.

Thus it appears that the mortality rate is initially high, diminishes progressively during the first 2 years of life, and increases again during the 3rd year, and that survival beyond the 3rd year can be ignored. This pattern of mortality can be conveniently represented by the multiple-rate exponential model and the data are summarized in Table 3 with calculated values of Z for each of the four periods into which the life cycle has been divided. For the purposes of this model, it has been assumed that the very high mortality rate occurs over the first 0.1 year, i.e., approximately up to hatching and development of the earlier larval stages.

Applying these data to the model for linear growth in length and multiple-rate exponential mortality provides the estimates of biomass and annual production given for each stage and for the total life span in Table 3. It appears that annual production from all stages of the life cycle is approximately 1.8 times the mean biomass. The greater part of both biomass and production is contributed by animals in their 2nd and 3rd years, and there is relatively little difference in the production–biomass ratio between these two stages. The production–biomass ratio is much higher for the first-year animals but these contribute so little to the absolute quantities that the ratio for this period has little effect on the overall result.

To examine this effect further, calculations have also been made for two other models. In one, the initial period of high mortality rate is assumed to extend over the first 3 months, with the same number of survivors remaining at this time (12,500) as after 0.1 year in the original model. The final model represents the extreme, but improbable, situation in which rapid mortality proceeds at a constant instantaneous rate ($Z = 5.991$) over the whole of the 1st year with 1250 survivors at the end. The results for all three models are summarized in Table 4. Since it seems very unlikely that the rapid mortality stanza would extend much beyond the first half year, the probable range of values for the production–biomass ratio seems to be about 1.8–2.3 with the lower end of the range being most likely.

It thus appears that Gulland's estimate of the production of krill in the Antarctic on the basis of a 1:1 ratio of annual production to mean biomass is probably about half the correct value. A better figure would probably be about 150 million tons, or more if the estimate of standing crop at 75 million tons is too low.

One final point may be noted: both Gulland (1970) and Hempel (1970) have assumed first, that the mean life span of krill is about 1 year, and then that,

TABLE 1. Formulae for total production and the biomass integral by time for cohorts represented by all possible combinations of the mortality and growth functions defined in text. The asterisk (*) in the ratio column indicates that no simplified formulation of the ratio between the original integrals has been found.

Mortality function	Growth function	Production (P)	Biomass integral (B*)	P/B*
Linear	Exponential	$\frac{N_0W_0}{GT}\left[e^{GT}-GT-1\right]$	$\frac{N_0W_0}{G^2T}\left[e^{GT}-GT-1\right]$	G
Linear	Linear (W)	$\frac{N_0W_T}{2}$	$\frac{N_0W_T\,T}{6}$	$\frac{3}{T}$
Linear	Linear (L)	$\frac{N_0W_T}{4}$	$\frac{N_0W_TT}{20}$	$\frac{5}{T}$
Linear	Prop. t^m (m integer)	$\frac{N_0W_T}{m+1}$	$\frac{N_0W_TT}{(m+1)\,(m+2)}$	$\frac{m+2}{T}$
Linear	Neg. exponential	$N_0W_\infty K\left[\frac{1}{K}-\frac{1}{K^2T}(1-e^{-KT})\right]$	$N_0W_\infty\left[T\left(\frac{1}{2}-\frac{1}{K}\right)+\left(\frac{1}{K^2}-\frac{1}{K}+\frac{T}{K}\right)(1-e^{-KT})\right]$	$\frac{K(K-1+e^{-K})}{\frac{K^2}{2}-K+1-e^{-K}}$
		or $N_0W_\infty-\frac{N_0W_T}{KT}$	*or* $N_0W_\infty T\left(\frac{1}{2}-\frac{1}{K}\right)+N_0W_T\left(\frac{1}{K^2}-\frac{1}{K}+\frac{T}{K}\right)$	
Linear	v. Bertalanffy	$N_0W_\infty\left[1+\frac{3}{KT}e^{-KT}-\frac{3}{2KT}e^{-2KT}+\frac{1}{3KT}e^{-3KT}-\frac{11}{6KT}\right]$	$N_0W_\infty\left[\frac{T}{2}-\frac{1}{K^2T}\left(3e^{-KT}-\frac{3}{4}e^{-2KT}+\frac{1}{9}e^{-3KT}\right)-\frac{1}{K}\left(\frac{11}{6}-\frac{85}{36KT}\right)\right]$	*
Fixed span	Exponential	$N_0W_0(e^{GT}-1)$	$\frac{N_0W_0}{G}(e^{GT}-1)$	G
		or $N_0(W_T-W_0)$	*or* $\frac{N_0}{G}(W_T-W_0)$	
Fixed span	Linear (W)	N_0W_T	$\frac{N_0W_TT}{2}$	$\frac{2}{T}$
Fixed span	Linear (L)	N_0W_T	$\frac{N_0W_TT}{4}$	$\frac{4}{T}$
Fixed span	Prop. t^m	N_0W_T	$\frac{N_0W_TT}{m+1}$	$\frac{m+1}{T}$
Fixed span	Neg. exponential	N_0W_T	$N_0\left[W_\infty T-\frac{W_T}{K}\right]$	$\frac{K\,W_T}{W_\infty KT-W_T}$
Fixed span	v. Bertalanffy	N_0W_T	$N_0W_\infty\left(T-\frac{11}{6K}+\frac{3e^{-KT}}{K}-\frac{3e^{-2KT}}{2K}+\frac{e^{-3KT}}{3K}\right)$	*

Exponential (single)	Exponential	$\frac{N_0W_0}{G-Z}(e^{(G-Z)T}-1)$	$\frac{N_0W_0}{G-Z}(e^{(G-Z)T}-1)$	G
		or $\frac{G}{G-Z}(N_TW_T-N_0W_0)$	*or* $\frac{1}{G-Z}(N_TW_T-N_0W_0)$	
Exponential (single)	Linear (W)	$\frac{N_0W_T}{ZT}$	$\frac{N_0W_T}{Z^2T}$	Z
Exponential (single)	Linear (L)	$\frac{6N_0W_T}{Z^3T^3}$	$\frac{6N_0W_T}{Z^4T^3}$	Z
Exponential (single)	Prop. t^m	$\frac{m!N_0W_T}{Z^mT^m}$	$\frac{m!N_0W_T}{Z^{m+1}T^m}$	Z
Exponential (single)	Neg. Exponential	$\frac{KN_0W_\infty}{Z+K}$	$\frac{KN_0W_\infty}{Z(Z+K)}$	Z
Exponential (single)	v. Bertalanffy	$3KN_0W_\infty\left(\frac{1}{Z+K}-\frac{2}{Z+2K}+\frac{1}{Z+3K}\right)$	$N_0W_\infty\left(\frac{1}{Z}-\frac{3}{Z+K}+\frac{3}{Z+2K}-\frac{1}{Z+3K}\right)$	Z
Exponential (multiple)	Exponential	$G\sum^N\frac{S_nW_n-S_{n-1}W_{n-1}}{G-Z_n}$	$\sum^N\frac{S_nW_n-S_{n-1}W_{n-1}}{G-Z_n}$	G
		or $G\sum^N\frac{B_n-B_{n-1}}{G-Z_n}$	*or* $\sum^N\frac{B_n-B_{n-1}}{G-Z_n}$	
Exponential (multiple)	Linear (W)	$\frac{W_T}{T}\sum^N\frac{D_n}{Z_n}$	$\frac{W_T}{T}\left\{\sum^N\frac{D_n}{Z_n^2}-\sum^N\frac{1}{Z_n}(S_nT_n-S_{n-1}T_{n-1})\right\}$	*
Exponential (multiple)	Linear (L)	$\frac{3W_T}{T^3}\sum^N(S_{n-1\ n-1}R_n-S_{n\ n}R_n)^\dagger$	$\frac{W_T}{T^3}\sum^N(S_{n-1\ n-1}Q_n-S_{n\ n}Q_n)$	*
Exponential (multiple)	Prop. t^m	$\frac{m-1!\,W_T}{T^m}\sum^N\left\{S_{n-1}\left(\frac{T_{n-1}^m}{m-1!Z_n}\cdots\frac{1}{Z_n^m}\right)-S_n\left(\frac{T_n^m}{m-1!Z_n}\cdots\frac{1}{Z_n^m}\right)\right\}$	$\frac{m!W_T}{T^m}\sum^N\left\{S_{n-1}\left(\frac{T_{n-1}^m}{m!Z_n}\cdots\frac{1}{Z_n^{m+1}}\right)-S_n\left(\frac{T_n^m}{m!Z_n}\cdots\frac{1}{Z_n^{m+1}}\right)\right\}$	*
Exponential (multiple)	Neg. exponential	$W_\infty K\sum^N\frac{1}{Z_n+K}(S_{n-1}e^{-KT_{n-1}}-S_ne^{-KT_n})$	$W_\infty\sum^N\left(\frac{S_ne^{-KT_n}-S_{n-1}e^{-KT_{n-1}}}{Z_n+K}-\frac{S_n-S_{n-1}}{Z_n}\right)$	*
Exponential (multiple)	v. Bertalanffy	$3W_\infty K\sum^N\left(\frac{S_{n-1}e^{-KT_{n-1}}-S_ne^{-KT_n}}{Z_n+K}-\frac{2(S_{n-1}e^{-2KT_{n-1}}-S_ne^{-2KT_n})}{Z_n+2K}+\frac{S_{n-1}e^{-3KT_{n-1}}-S_ne^{-3KT_n}}{Z_n+3K}\right)$	$W_\infty\sum^N\left(\frac{S_{n-1}-S_n}{Z_n}-\frac{3(S_{n-1}e^{-KT_{n-1}}-S_ne^{-KT_n})}{Z_n+K}+\frac{3(S_{n-1}e^{-2KT_{n-1}}-S_ne^{-2KT_n})}{Z_n+2K}-\frac{S_{n-1}e^{-3KT_{n-1}}-S_ne^{-KT_n}}{Z_n+3K}\right)$	*

$^\dagger{}_{n-1}R_n=\frac{T_{n-1}^2}{Z_n}+\frac{2T_{n-1}}{Z_n^2}+\frac{2}{Z_n^3}$; $_{n-1}Q_n=\frac{T_{n-1}^3}{Z_n}+\frac{3T_{n-1}^2}{Z_n^2}+\frac{6T_{n-1}}{Z_n^3}+\frac{6}{Z_n^4}$

TABLE 2. Comparison, for each mortality function examined, between mean age, mean life span, and the production–biomass ratios for each growth function. The more complex ratios are shown simply as functions of the parameters concerned. Asterisks (*) mark the ratios that are equal to the reciprocal of the mean age for the same mortality function. No ratios are equal to the reciprocal of the life span unless mean life span and mean age are themselves equal.

Mortality function	Production–biomass ratio for growth functions: Neg. exponential	von Bertalanffy	Linear in wt	Linear in length	Prop. to t^m	Exponential	Mean age	Mean life span
Linear	$f(k,T)$	$f(k,T)$	$\frac{3^*}{T}$	$\frac{5}{T}$	$\frac{m+2}{T}$	G	$\frac{T}{3}$	$\frac{T}{2}$
Fixed span	$f(k,T)$	$f(k,T)$	$\frac{2^*}{T}$	$\frac{4}{T}$	$\frac{m+1}{T}$	G	$\frac{T}{2}$	T
Exponential (single rate)	Z*	Z*	Z*	Z*	Z*	G	$\frac{1}{Z}$	$\frac{1}{Z}$
Exponential (multiple rate)	$f(k,Z)$	$f(k,Z)$	$f(Z)^*$	$f(Z)$	$f(Z)$	G	$\frac{\sum^N \frac{D_n}{Z_n^2} - \sum^N \frac{T_n S_n - T_{n-1} S_{n-1}}{Z_n}}{\sum^N \frac{D_n}{Z_n}}$	$\sum^N \frac{D_n}{Z_n}$

TABLE 3. Calculation of the ratio between cumulative production (P) and the biomass integral by time (B*) for a hypothetical krill population starting with 1000 breeding females and assuming linear growth in length and exponential mortality within each period. Production and biomass are in units of the weight of one individual at one year old.

Time (*years*)	No. survivors	Z	Period P	Period B*	P/B*	ΣP	ΣB*	ΣP/ΣB*
0	500000	–	–	–	–	–	–	–
0.1	12500	36.89	.085	.002	53.25	.085	.002	53.25
1.0	1250	2.558	5.412	1.150	4.71	5.497	1.151	4.77
2.0	625	.693	11.690	6.055	1.93	17.187	7.206	2.38
3.0	62	2.303	8.018	6.364	1.26	25.205	13.570	1.86

TABLE 4. Proportion of total production and of the biomass integral accumulated in 1 year for model krill populations with the rapid growth period extending through 0.1, 0.25, and 1.0 years. The ratio of total production to total biomass integral is also shown.

Model	Rapid growth period (*years*)	Proportion of total P in year 1	Proportion of total B* in year 1	$\sum P/\sum B^*$
I	0.1	.218	.085	1.86
II	0.25	.276	.100	1.97
III	1.0	.570	.240	2.79

as a consequence of this, the annual production is about equal to the average standing crop. It has been shown above that the annual production is likely to be more nearly twice the mean standing crop. From the same models the mean life span and the mean age can also be calculated. For model I, for example, these are 0.037 and 0.21 years respectively. The true mean life span is much smaller than that suggested by Gulland and Hempel because it must take into account the very large number of animals that die at an early age, and are probably underestimated in studies based on plankton net catches or on whale food. Use of the true mean life span as an estimate of the reciprocal of the production–biomass ratio would, in this instance,

cause production to be overestimated by a factor of about 14. The principle, noted in the general discussion, that the mean age provides a better estimate of the ratio, applies here also, and the overestimation is only by a factor of about 2.5.

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Radioisotope X-Ray Fluorescence Spectrometry in Aquatic Biology: A Review

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CALAPRICE, J. R., H. M. MCSHEFFREY, AND L. A. LAPI. 1971. Radioisotope X-ray fluorescence spectrometry in aquatic biology: a review. J. Fish. Res. Bd. Canada 28: 1583–1594.

X-ray fluorescence spectrometry is described as an efficient means of carrying out non-destructive qualitative and quantitative chemical analyses of inorganic substances. A brief review is presented on the way in which this methodology was developed to recognize marked individuals and its application towards determining the geographic origin of organisms using multivariate analysis of the trace element composition of untagged animals. In addition, the results of experiments in which 34 species of invertebrates were compared and different parts of the same organisms irradiated, demonstrated that organisms may possess characteristic elemental compositions that are species specific. Multiple discriminant function analysis of the data showed that species may be classified on the basis of their chemical composition with few errors. Winter and summer growth of molluscan shells were distinguishable by the same method of elemental analysis, and a method for determining the age of organisms is given. Stepwise discriminant function analysis of the groups of elemental standards demonstrate that it is possible to isolate the most significant differences found between the groups compared by this methodology. The importance of these findings to studies in biogeochemistry, physiology, and pollution are briefly reviewed. X-ray fluorescence spectrometry is considered to be one of a number of related forms of data acquisition systems, each with broad applications.

CALAPRICE, J. R., H. M. MCSHEFFREY, AND L. A. LAPI. 1971. Radioisotope X-ray fluorescence spectrometry in aquatic biology: a review. J. Fish. Res. Bd. Canada 28: 1583–1594.

Les auteurs décrivent la spectrométrie à fluorescence par rayons X comme méthode efficace et non destructrice d'analyse qualitative et quantitative de substances inorganiques. Ils passent brièvement en revue le développement du protocole suivi pour l'identification d'individus marqués et son application, par le biais d'études multivariables des oligoéléments d'animaux non marqués, à la détermination du lieu d'origine des organismes. La comparaison de 34 espèces d'invertébrés et l'irradiation de plusieurs parties d'un même individu donnent à entendre que ces organismes possèdent une composition élémentaire spécifique. L'étude des fonctions discriminantes multiples des données indique que l'on peut, sans trop d'erreur, classer les espèces d'après leur composition chimique. Au cours d'une seconde série d'essais, l'analyse élémentaire a également permis de différencier la croissance d'hiver de celle d'été des coquilles de mollusques. Suit la description d'une méthode d'évaluation de l'âge des organismes. L'étude des fonctions discriminantes en gradins démontre la possibilité d'isoler les différences les plus marquées entre les groupes comparés suivant cette méthode. Les auteurs soulignent l'importance de leurs découvertes sous le rapport des études biogéochimiques, physiologiques et de pollution. D'après eux, la spectrométrie à fluorescence par rayons X est un système, parmi plusieurs, d'acquisition de données, chacun possédant une gamme étendue d'applications.

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RECENT advances in technology suggest new methods of dealing with classical problems in biology. Data gathered by electronic acquisition systems are often more voluminous, more complete, and more reliable than those gathered by conventional methods. In addition, such data are in a form that is compatable with computers. Data acquisition systems and computers can be brought together and molded into a methodology that provides the investigator with the option of considering approaches that have previously been deemed impractical. In this report we will be concerned with the use of one such system, radioisotope X-ray fluorescence, as a tool for studying classical biological problems. Differences in the chemical composition of organisms, or parts of organisms, are characterized electronically by nondestructive analysis and provide the basic data. As a means of acquainting biologists with the technique, the nature of radioisotope X-ray fluorescence analysis is described. This is followed by applications in the areas of fisheries, population biology, taxonomy, and in pollution.

Radioisotope X-Ray Fluorescence Spectrometry

X-ray fluorescence spectroscopy is a method of elemental analysis, based on the energetic states of the electron orbitals of atoms. It enables one to detect the presence of a wide variety of chemical species without having to prepare or destroy the sample. The apparatus required is relatively simple and inexpensive.

The methodology is best understood by considering the structure of the atom. The working hypothesis is that the atom consists of a heavy, positively charged nucleus, consisting of protons and neutrons and negatively charged electrons in orbits around the former. These electrons are arranged in a specific series of shells, orbitals, and suborbitals. Each electron from each orbit is associated with a discrete energy state. When exposed to bombardment of sufficient energy, the electrons may absorb this energy and escape from their orbits. The probability of such an occurrence is dependent on the difference in energy of the source and that of the particular orbital state. This probability increases as the energy of the source decreases until it equals the absorption edge or energy associated with excitation of the electron, and drops abruptly to zero as it decreases further. Electrons from less stable orbitals or free electrons may fill these vacated positions with the concomitant release of a discrete amount of energy in the form of electromagnetic radiation. These radiations are termed X-rays due to their origin in electron transition within the atom. The energies of these emissions can be calculated from a theoretical knowledge, derived from quantum theory, of the energy states associated with the electron orbitals for each atom. The reader is referred to textbooks of modern physics for a more thorough treatment of atomic structure and quantum mechanics (Leighton 1959).

If one can detect and measure the energies of the X-rays produced when a sample of material is exposed to a high energy source, one can determine their elemental origin by reference to a table of known emission energies. Because these emission energies are discrete, one can determine the presence of many elements simultaneously.

Figure 1 is a schematic representation of the X-ray fluorescence spectrometry equipment in use at the Fisheries Research Board, Biological Station in Nanaimo. A synthetic radioisotope, Americium^{241}, is used as the primary energy source as its long half-life, 458 years, provides a relatively constant intensity. This isotope emits predominantly gamma rays at 59.6 keV, thus the electrons of any element with an absorption edge below this energy could be excited. A secondary source, or target, may be included such that the radiation from the Americium strikes the target with the associated production of characteristic X-rays, at a lower energy. In either case, the geometry of the source holder is arranged such that the energy is beamed towards the sample. The electrons of the sample are excited and the X-rays produced pass through the annular source holder to strike the detector, a lithium-drifted silicon semiconductor. The resulting pulse is amplified, shaped, and passed to the pulse height analyzer. In this component, the energy range of interest is selected and divided into a series of from 100–400 channels of equal energy interval. Each pulse received is categorized in terms of its energy, which is directly related to the X-ray emission energy, and stored in the appropriate channel of

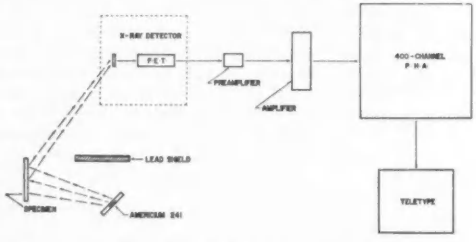

FIG. 1. Schematic arrangement of radioisotope X-ray fluorescence spectrometer in current use. That part of the system outlined in broken lines is cooled by liquid nitrogen.

the analyzer. This information may be manipulated, displayed on an oscilloscope, and, at the end of a preselected time period, printed and punched on paper tape by a teletype. Other output devices may be used. The system is fully automated, from sample changing to data output, leaving the operator free for sample preparation and data analysis.

Qualitative and Quantitative Chemical Analysis

Figure 2 is a plot of the data obtained from analyzing a mixture of known elements by X-ray fluorescence analysis. For each element two peaks are evident, the result of electrons from the L (K alpha), and M (K beta) shells filling the vacancy left by excitation of electrons from the K shell of each atom. No emissions were detected from the L shells of these elements, as the energy used to excite the electrons was high, and the probability of absorption of this energy by electrons in the L shell consequently very low. This figure also demonstrates the determination of the presence of several elements simultaneously.

The emission energy of a channel peak can be determined from the graph (Fig. 3), which was drawn from the analysis of elements with emissions at known energies. From this, it can easily be seen how qualitative elemental analysis is carried out, by relating peak energy to known emission energies, and then referring to the values tabulated for the different elements (Clark 1963). This process of qualitative analysis can be fully automated.

Quantitative analysis is also possible by X-ray fluorescence analysis. Ideally, one could simply relate the number of counts in a particular channel, the emissions at a particular energy, with the concentration of the element responsible. Unfortunately, when using X-ray fluorescence methods for analytical determinations one must consider matrix effects. These effects cause the intensity of fluorescent radiation from an element to vary, not only as a function of its own concentration, but also as a function of the concentration of those other elements within the matrix.

A number of methods have been proposed to deal with this problem. One such method uses the information derived from Compton backscatter radiations. If efficient excitation radiation is used, the ratio of the backscatter peak to the characteristic radiation of the element is nearly independent of matrix effects (Rhodes 1967). The method requires high resolution so that characteristic peaks do not overlap. Different methods of sample preparation

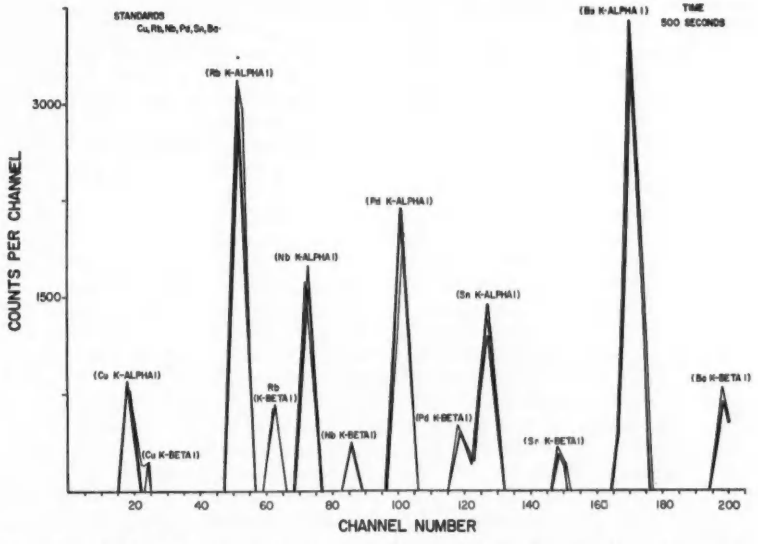

FIG. 2. Display of peaks obtained by analyzing a mixture of known elements by X-ray fluorescence analysis. Each element is evidenced by two peaks; a K_α due to electron transfer from the L shell into the K shell and a K_β peak due to transition from the M shell. The background peaks have been subtracted for the sake of clarity. The height of the peak is due to the number of emissions at this energy.

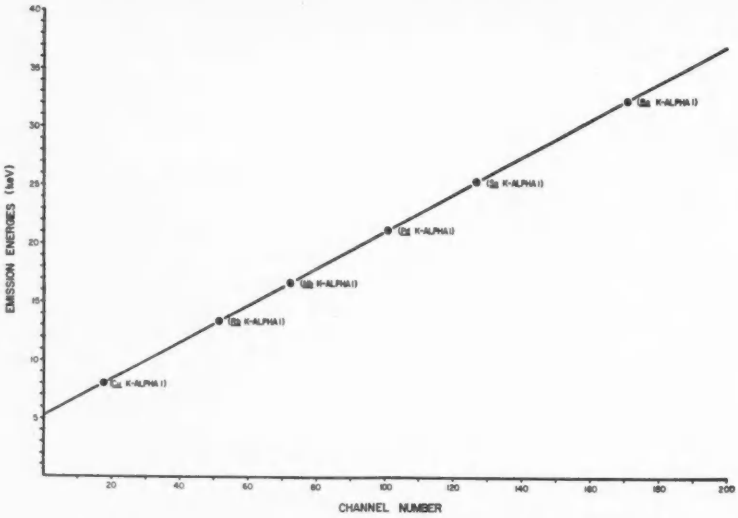

FIG. 3. Relation between channel number and emission energy as calibrated from the position at which known elements appear in the spectrum. The energy, and element responsible, of an unknown peak can be determined by using this relation and referring to tabulated values for the elements (Clark 1963).

have also been tried. Among some of the more effective methods have been dilution and thin film preparation (Carr-Brion and Payne 1970). Dilution of the sample with powders, liquids, or glasses reduces the absorption effects of the sample and gives all samples approximately the same matrix; this allows for easy preparation of standards. Samples prepared as thin films are virtually independent of matrix effects due to absorption. Mathematical and theoretical approaches to matrix corrections have also been tried. One approach, which is semitheoretical, is based upon differences in the mass absorption coefficient of the elements in the matrix and has been successful in the soft X-ray region, but the effectiveness of the method in the hard X-ray region is uncertain (Anderman 1966). The fundamental parameter method is an approach that seems to have broad application (Birks 1969; Criss and Birks 1968). In this method one must know the spectral distribution of the excitation source, the mass absorption coefficients, and the fluorescent yields. A set of simultaneous equations are written for the characteristic radiations of the elements in the matrix and are solved by iteration. The accuracy of this method appears to be limited only by how well the parameters are known. Another mathematical approach makes use of multiple regression analysis (Alley and Myers 1965). This method is well suited for biological studies, for a large number of different elements may contribute to such matrices. Standards, samples composed of known concentrations of the elements, are prepared. Sets of simultaneous equations that relate the concentration of each element to the observed X-ray intensities are derived. These coefficients that characterize the interelemental effects are then used to arrive at the adjusted X-ray intensities and hence the concentration.

One point must be stressed: the methods of radioisotope X-ray fluorescence spectrometry can be fully automated to render qualitative and quantitative analysis. The minimum detectable concentration of each of the elements in the sample depends upon the intensity of the radioactive source used to excite the sample, the counting time, and the efficiency of excitation. Investigators report detecting heavy metals in the parts per billion range (Woldseth et al. 1971; Anspaugh et al. 1967). We might consider this methodology in biology, whenever one is confronted with a large number of chemical analyses, and when information on one or more chemical elements is desired.

Organisms of the Same Species Possess Chemoprints Identified by Chemical Analysis

The equipment referred to in this report had originally been obtained to read microtags that

were developed to overcome the problems involved in tagging small animals. These microtags consisted of small amounts of elements in various combinations and concentrations that were suspended in silicone rubber. These mixtures and the inert medium were injected subcutaneously into fish fry (Calaprice and Calaprice 1970). In this application, fish would be allowed to mingle freely in a laboratory or field situation and be rapidly identified later by X-ray fluorescence spectroscopy. Figure 4 demonstrates the X-ray emission pattern observed by analysis of a tagged animal. In addition to the peaks from injected elements, each organism gave rise to a series of emissions, peaks, and Compton background, due to their natural chemical and physical make-up. A natural tag, or chemoprint, was suggested by this observation, possibly due to the elements it had picked up from the environment. This led to the prospect that one could differentiate groups of animals from different geographic areas by analyzing the data obtained from X-ray fluorescence spectroscopy using multivariate statistical methods. In the analysis considered, one could derive a series of discriminant functions that best separate groups on the basis of the X-ray fluorescence data, and if significant, the results of the analysis would be used to classify unknown individuals into specific groups according to computed probabilities for membership (Cooley and Lohnes 1962; Seal 1964).

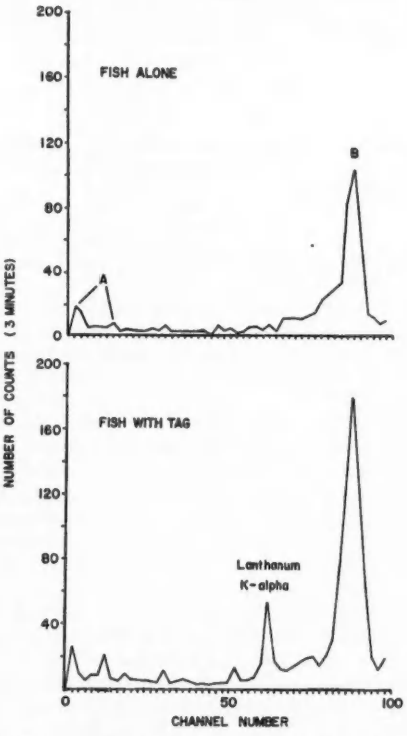

FIG. 4. X-ray emission spectra for tagged and untagged sockeye salmon, *Oncorhynchus nerka*. A and B represent background peaks. Those marked A are from the lead shielding and B is backscatter from a thulium target used in this study.

In a preliminary report, Calaprice (1970) detailed this prospect, and described how these techniques were used in a comparison of sockeye and coho salmon smolts from various river systems in British Columbia and Alaska. In that study samples of juvenile coho and sockeye salmon were collected from different geographic areas, and preserved samples were characterized by these methods of chemical and statistical analysis. The chemical spectra of groups were found to differ significantly, and on the basis of computed probabilities were assigned to area of origin with few errors.

In a subsequent publication (Calaprice 1971), the results of a similar comparison of different life stages of sockeye salmon were described. The analysis of sockeye salmon fry and adult collections from different areas revealed that differences exist among populations of each of the different life stages, that is, differences existed between fry from different regions as well as adults from different regions. Differences among the adults are particularly interesting, for these results indicate that this methodology may be useful in determining the area of freshwater origin for salmon taken in the fishery. This application need not be restricted to salmon, or to adults, for differences were found among juveniles from different geographic areas.

A program is currently in progress to examine coho salmon smolts and adults from various river systems along the Pacific coast, to determine which elements are important in discriminating populations, and with a view to predicting the most probable destinations of those animals caught in the commercial fishery.

Chemo-Taxonomy, Spectra may also be Species Specific

The comparison of juvenile sockeye and coho salmon smolts from different regions is interesting in another respect. The chemical differences associated with geographic areas were not as great as were differences between the two species (Fig. 5). As a means of testing the hypothesis that X-ray spectral data could be used to classify organisms

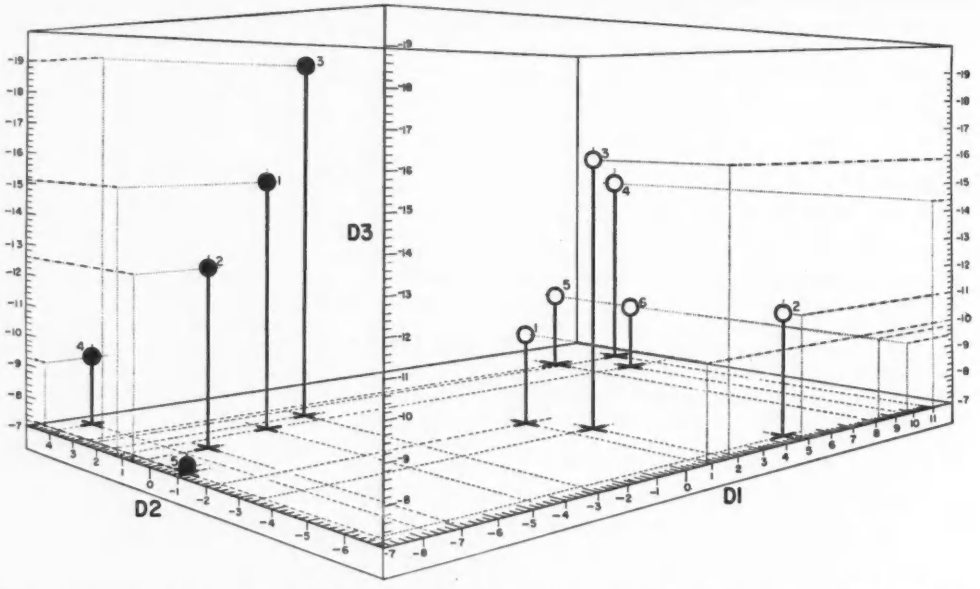

FIG. 5. Position of sockeye, *Oncorhynchus nerka* (●), and coho salmon, *O. kisutch* (○), smolts in three dimensional discriminant space. D_1, D_3, D_2 are the first three discriminant axes. The location of the spheres indicates the position of the means of samples from different geographic areas (Calaprice 1970).

with the above, and statistical methods similar to those suggested by Sokal and Sneath (1963), a total of 413 individuals from 34 species of invertebrates were irradiated for 5 min each. The analysis was carried out on preserved organisms obtained from the museum at the Nanaimo Biological Station; the species used, sample sizes, and parts irradiated are given in Table 1.

As in the published studies, the X-ray data were subjected to a stepwise discriminant function analysis. The results indicate that the spectra of the groups compared are statistically distinct; F with 2079 and 9592 degrees of freedom = 4.85, $P < 0.0001$. Comparisons were made between all possible combinations of the different species, and these demonstrated that of the 561 possible comparisons, 99.3% of the comparisons were found to be statistically distinct with $P \leq 0.05$. There were 98.5% of the comparisons significant at the 0.0001 level. Only four comparisons (0.7%) were statistically insignificant. One species of chiton, *Tonicella lineata*, was not statistically different from two other species of chitons, *Cryptochiton stelleri* and *Katherinia tunicata*; one limpet, *Acmea personna*, was not differentiated from one urchin, *Strongylocentrotus drobachiensis*; and two species of brittle stars, *Ophiomusium lymani* and *Ophiopholis aculeata*, were not separated.

As in most studies, sample size is related to statistical significance, and one should probably not place a great deal of importance on those few instances where significance was not found, considering the small sample sizes used in the study.

The second form of evidence suggesting that this methodology may be useful to taxonomists comes from the reclassification of the samples used to derive the functions. Of the 413 individuals irradiated, only 15 or 3.6% of the total number were misclassified. It is tempting to speculate further and contrast the observed chemical similarities among the groups with the known taxonomic relations. Although the results of the stepwise analysis and the plot of the first two canonical correlates suggest a relation, the question of affinities should be left to a detailed analysis using the more appropriate methods suggested by Sokal and Sneath (1963).

Can Organisms be Aged by Irradiating Hard Parts

We have also considered the possibility of using these techniques to age marine organisms. Specimens

TABLE 1. List of invertebrate species compared, areas irradiated, and sample sizes.

Sample	Area irradiated	Sample size
Eupentacta quinquesemita (sea cucumber)	Lateral area	13
Ctenodiscus crispata (starfish)	Arm	11
Pisaster ochraceous (starfish)	Central disc, dorsal surface	12
Ophiura sarsi (brittle star)	"	13
Gorgonocephalus caryi (brittle star)	"	12
Ophiomusium lymani (brittle star)	"	13
Ophiopholis aculeata (brittle star)	"	12
Strongylocentrotus franciscanus (urchin)	Test, outer surface	13
Strongylocentrotus drobachiensis (urchin)	Test, inner surface	12
Brisaster latifrons (urchin)	Test, inner surface	12
Cryptochiton stelleri (chiton)	Dorsal plate	12
Katherinia tunicata (chiton)	"	10
Tonicella lineata (chiton)	"	12
Thais emarginata (whelk)	Shell, outer surface, above lip	13
Thais canaliculata (whelk)	"	12
Thais lamellosa (whelk)	"	12
Searlisia dira (whelk)	"	12
Haliotis kamtschatkana (abalone)	Shell, outer surface	12
Acmea fenestrata (limpet)	Shell, outer surface, anterior area	13
Acmea digitalis (limpet)	"	12
Acmea personna (limpet)	"	13
Panope generosa (clam)	Shell, outer surface	11
Spisula falcata (clam)	"	12
Zirfaea gabbi (clam)	"	12
Lucinoma annulata (clam)	"	12
Pecten caurinus (scallop)	Shell, external surface	12
Laqueus jeffreyi (brachiopod)	Shell, outer surface	12
Cellaria borealis (bryozoan)	Entire	13
Corella inflata (tunicate)	"	13
Clavelina sp. (tunicate)	"	12
Sponge A	"	12
B	"	12
C	"	13
D	"	11

of the scallop (*Pecten caurinus*), an organism that is reportedly easy to age from the pattern of ridges in the shell and also the pattern of light and dark areas, were collected. Six different locations along the shell were selected, three summer and three winter. The lighter-colored area is believed to be summer growth and the dark area winter growth. Each location was irradiated a number of times to give a total of 60 spectra of summer growth and 80 spectra of winter growth. These data were used to derive one discriminant function separating winter and summer growth.

The processing of 199 variables in a stepwise discriminant function analysis in computers presents difficulties. To reduce the cost of the analysis and avoid costly program changes, the data were divided into three sets of 79, 80, and 40 variables. The results using the 79 variables indicated that only 10 of these variables contributed significantly to discrimination. The analysis of the second set of variables (80) yielded only 13 variables, and the third analysis yielded 3 variables. These "important" variables were then employed in a fourth analysis, in which all the significant variables from each section of the spectrum were employed. The results indicated even more redundancy in the data, for the number of significant variables was reduced to 11 out of the 199.

The results of the analysis using these 11 variables are interesting, in that they indicate that significant differences exist between what we have taken to be winter and summer growth, F with 12 and 128

df is 15.806 and the $P < 0.0001$. Furthermore, when these functions were used to classify the samples at the final step, 125 out of 140 or 89.3% were found to have been correctly classified. The curve in Fig. 6 illustrates the increase in correct classification as the number of steps increased.

Our ability to distinguish winter and summer growth suggests that aging may be accomplished by scanning across shells, or hard parts of organisms and noting the frequency with which winter and summer areas occur.

The Nature of Differences that Allow for Separation Among Groups

Difficulties of interpretation arise in multivariate analysis. The use of large numbers of variables and small sample sizes often result in solutions that are ambiguous. Whereas the statistical analysis of the data discussed concerns the spectra of the different groups, the results of the stepwise analysis does give some indication of the nature of the differences separating groups. One can determine the X-ray energies that give rise to those variables that emerge as discriminators (see Fig. 3). However, it is not always simple to relate these to specific elements, partly because of the low concentrations of these elements in tissue. As a means of studying the nature of chemical differences separating groups, different elements of known concentration were mixed with silicone rubber and were allowed to harden. Seven of these plasmodes were mixed and each sample was irradiated for 2 min. The same samples were irradiated 25 times, which gave a total of 175 different analyses.

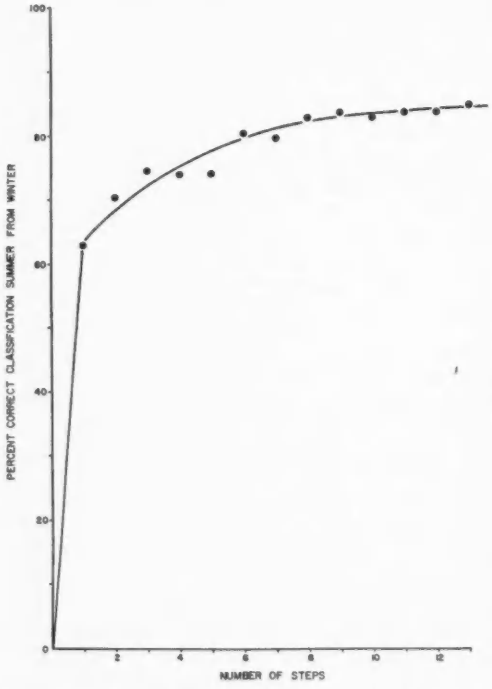

FIG. 6. Percent of the total number of winter and summer shell spectra that were correctly assigned in each successive step.

Again the analysis was conducted in four stages: the first three were analyses of separate sections of the spectrum, whereas the fourth used all those variables found to be significant in the first three analyses. The discussion of the data that follows will be restricted to this summary analysis. Significant differences were found among the groups compared ($F(240,775\ df) = 11.45$, $P < 0.0001$). Each of the seven groups that contained one different element in the same silicone matrix differed significantly from one another. In addition a high degree of discrimination was reached. Only 11 out of 175 samples were misclassified, or 93.6% were correct.

The results of the stepwise analysis are summarized in Table 2. We note that 40 steps were chosen, that is, 40 variables out of the 199 contributed significantly to the discrimination. The ordering of the variables is significant, the first variable explains more of the variance than the second, and the last variable, although when included it does increase the power of discrimination, is the least important discriminator. The energy associated with each variable was determined from the standard equation and this in turn was used to arrive at the chemical element most likely associated with that channel. These results indicate that the channels chosen correspond in most instances to the K_α X-rays of the element as well as to backscatter peaks.

As a means of testing this hypothesis again, a new set of plasmodes were irradiated and analyzed. Five different elements were chosen and each sample analyzed repeatedly. The discriminant analysis revealed that significant differences existed between the spectra of the different elements ($F(72,387\ df) = 21.75$, $P < 0.0001$). In this instance only one out of 120 samples was misclassified, or 99.3% were correct. The results of the stepwise analysis (Table 3) again reveal that backscatter peaks were chosen as well as the channels associated with the peaks of the different elements.

TABLE 2. Summary of stepwise discriminant analysis of elemental standards As, Br, Zn, Pd, Cd, Sb, and Cs (0.01% of the oxide by weight in silicone rubber). The variable number, energy in keV, probable elemental source of X-rays, groups separated, and % correct classification of the samples are given for each step.

Step no.	Channel no.	Energy (*keV*)	Probable elemental source	Groups separated in paired comparisons	% correct classification
1	40	11.7	Br K_α	Bromine from others	27.4
2	165	31.2	Cs K_α	Cesium from others	36.6
3	164	31.0	Cs K_α	Further separates cesium helps separate Zr from others	44.5
4	163	30.9	Cs K_α	Further separates Cs	50.8
5	127	25.3	Background	(Cd+Sb) from (As, Zr+Pd)	55.4
6	41	11.9	Br K_α	Further separates Br	65.1
7	161	30.6	Cs K_α	No apparent influence	62.9
8	125	24.9	Background	Again (Cd+Sb) from (As, Zr+Pd)	67.2
9	162	30.1	Cs K_α	No apparent influence	68.5
10	11	7.2	Background	Helps separate (Zr+Pd) from As and from Sb	72.5
11	188	34.8	Cs K_β	No apparent influence	–
12	6	6.4	Background	Separates Pd from As+Zr	73.1
13	39	11.6	As K_β or Br K_α	No apparent influence	–
14	126	25.1	Background	"	–
15	42	12.1	Br K_α	"	–
16	32	10.5	As K_α	Separates As from Zr	–
17	112	22.9	Cd K_α	Helps separate Cd from Sb	–
18	23	9.1	Background	Further separates As from Zr	–
19	64	15.5	Zr K_α	Further separates Zr from Pd	–
20	101	21.3	Pd K_α	Further separates Pd from Zr	85.1
21	60	14.9	Background	Further separates Pd from Zr	–
31	75	17.2	"	Helps separate Sb from Cd	–
32	90	19.5	"	Helps separate Sb from Cd	–
40	123	24.7	"	Further separates Sb from Cd	93.6

TABLE 3. Summary of stepwise discriminant analysis of elemental standards I, Ag, Zn, Cu, and Ba (approx 0.01% of oxide by weight). (See Table 2.)

Step no.	Channel no.	Energy (*keV*)	Probable elemental source	Groups separated in paired comparisons	% correct classification
1	106	22.2	Ag K_α	Separates Ag from all others	41.6
2	127	25.5	Sn K_α	Separates (Cu+Zn) from (I+Ba), and Cu from Zn	64.1
3	145	28.2	I K_α	Further separates Cu from Zn	72.5
4	169	31.9	Ba K_α	Separates Ba from I	83.3
5	171	32.1	Ba K_α	Completes separation Ba from I	89.1
6	124	24.9	Background	Further separates Cu from Zn	91.6
7	128	25.7	Background	No apparent effect	92.4
8	105	22.0	Ag K_α	"	93.2
9	104	21.8	Ag K_α	"	95.0
10	170	32.1	Ba K_α	"	95.7
11	107	22.3	Ag K_α	"	
12	88	19.4	Background	"	
13	146	28.5	"	"	
14	92	19.9	"	"	
15	148	28.9	I K_α	"	98.3
16	119	24.2	Ag K_β	"	
17	144	28.1	I K_α	"	
18	9	7.0	Background	"	99.2

All computations were carried out at the University of British Columbia (IBM 360-67) using BIOMED programs, Dixon (1970).

Discussion

The purpose of this report has not been to present detailed results and analysis of data, but to review the ways in which we have been using X-ray fluorescence spectrometry in our laboratory. The experiments that were described briefly were pilot studies, and the results of detailed studies will most likely be reported at a later time.

Essentially the system of electronics gathers data that may be processed to yield information on the inorganic composition of the sample. The instrumentation is sensitive enough to detect elements in the parts per million range, and in one instance, investigators report detecting mercury in fish tissue in parts per billion (Woldseth et al. 1971). This sensitivity coupled with the features of nondestructive analysis, little or no sample preparation, and simultaneous analysis of numerous elements, renders the system useful for many applications. Furthermore, automatic sample changing, magnetic storage and transfer of data, and high system reliability are features that enable one to gather data accurately and with little effort. In effect, the system provides a very useful method of acquiring the chemical data that biologists and biochemists deal with. In addition to standard chemical analysis, Mr F. Bernard of the Nanaimo Biological Station has found the method useful for labelling and tracing physiological products in molluscs (personal communication). He fed oysters encapsulated oxides of the rare earths and determined the pattern of feeding behavior and transport of food particles. In this way the methods were used as a form of nonradioactive tracing. This technique would appear to have definite advantages over the use of radioactive tracers, especially in physiological studies.

In a sense, the tagging methods developed by Calaprice and Calaprice (1970) are related, but in this application, elements (the tags) were localized in inert silicone rubber. The sensitivity of the apparatus made it possible to use small tags (less than 1 mm^3), implanted within the tissue where they remain invisible to predators, and to read the tags in live organisms with amounts of radiation less than that used in medical diagnostics. This method of "reading" tags is general and, since these initial studies, has been used to detect lactate compounds of several elements fed in low concentrations to fish. Other methods of chemical marking, i.e., incorporating elements in tissue by immersing and spraying are possible and offer the investigator a choice of approaches.

The ability to detect a number of trace elements at background levels within the tissue suggested that organisms possess "natural tags," which have been described as chemoprints. This possibility has been studied by other investigators using neutron-activation techniques (Devine and Peterle 1968; Fisheries Agency of Japan 1967) and by other more conventional methods of analysis (Hanson and Jones 1968). A good deal of the success enjoyed by Calaprice (1970, 1971) must be attributed to several factors: the method of analysis, instrumentation, and the statistical methods used in dealing with numerous variables.

The fact that geographic variation in the chemical spectra was less than that observed between the two species of salmon compared in an earlier experiment led, as stated, to the hypothesis that the methodology might be useful in taxonomic studies. The comparison of the different species of invertebrates described supports this prospect. In these studies no attempt was made to irradiate homologous organs; instead, the surface tissues of the organisms were irradiated. In one sense this may be taken as a weakness of the study, for unlike tissues of the same organism are known to accumulate elements in different concentrations (see Anon. 1955). On the other hand, the morphological differences that lead taxonomists to arrive at the present classification of organisms are based upon unique arrangements of tissue that result in morphological variation. In this respect, we have examined the different species chemically in much the same manner as the taxonomist examines them visually, usually beginning with the exterior of the organisms. Because different species are known to accumulate elements in varying concentrations (Vinogradov 1953), we must also consider attributing the chemical specificity we observed to this factor, as well as having looked at different arrangements of tissues. In any event, it appears possible to classify organisms with few errors using this methodology. Since classification is one of the aims of taxonomy, it would appear that one might be able to reduce the present level of expertise required in that aspect of the discipline. A chemical taxonomy of species is quite feasible using the methods of numerical analysis (Sokal and Sneath 1963), and it remains to be discovered how this taxonomy will compare with classical methods and whether it will be ultimately useful. One definite advantage of the electronic methods described is that the system can be operated remotely. This suggests that organisms can be identified and perhaps counted without human intervention.

Population studies often require a knowledge of the age distribution of the organisms comprising the group under study. Numerous methods have been devised to estimate this important population parameter. We have shown how X-ray spectrometry may be used to arrive at the age of organisms. The physiological basis for this is well known. Geographical and seasonal differences in the elemental composition of mollusk shells has been studied by a number of workers (see Pilkey and Goodell 1963). The differences in spectra that were noted are based upon chemical differences similar to those documented by these authors. At this stage it is not known if hard parts in different organisms such as fish and marine mammals differ as well. It seems likely that these or similar methods may be optimized to age a variety of organisms.

The analysis of plasmodes, elements mixed in a silicone rubber matrix, shows that it is possible to arrive at the chemical nature of the groups being compared. The stepwise discriminant function analysis demonstrated the chemical basis for subtle differences in spectra. This is normally difficult to achieve at low concentrations because of the redundancy in the system and the statistical errors due to counting X-rays. Each element may give rise to numerous peaks in the spectrum in addition to background peaks. The number of counts per channel may also deviate due to random counting errors. In addition to the above factors there are matrix effects, all of which give complexity to the spectra of the groups compared. This ability to reduce the spectra to its elemental basis suggests other applications. Organisms from different areas may be compared in geochemical surveys, compared for the presence of above "background" levels of inorganic pollutants, and so on. In this respect, the results of the stepwise discriminant function analysis for the aging study show that the differences found between summer and winter segments of a shell agree with differences expected from experimental studies. The stepwise results of comparing species also suggest what may prove to be concentrations of specific elements by different species.

The above results and discussion stem from applying what may be classified as one form of an electronic data acquisition system. Other systems such as laser spectroscopy and nuclear magnetic resonance are possible. Essentially the systems are similar in that they are composed of sensors that generate a signal and units of logic that allow one to translate these signals to useful data. These methods can be made reliable and efficient and will undoubtedly find many uses in biology. We have shown how the same system can be used to gather many diverse types of biological data, and it is quite probable that the same set of data will be useful for a number of purposes.

Acknowledgments

The authors thank Mr F. Bernard of the Nanaimo Biological Station for his many suggestions regarding the aging of organisms and for assistance throughout these studies. Dr C. Berkeley commented on the initial use of the methodology for taxonomic studies and provided samples of rhododendron species used in an initial pilot study.

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Evolution of the Chondrophora: Evidence from Behavioural Studies on *Velella*

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Fields, W. G., and G. O. Mackie. 1971. Evolution of the Chondrophora: evidence from behavioural studies on *Velella*. J. Fish. Res. Bd. Canada 28: 1595–1602.

The chondrophore *Velella* shows concert behaviour closely resembling and presumably homologous to that described for *Porpita*, *Pelagohydra*, and for the sessile tubularian hydroids *Tubularia* and *Corymorpha*. The movements consist of orally directed tentacular flexions, accompanied by retraction of the blastostyles, along with muscular contractions in the mantle and in the crest surmounting the sail. Concerts may consist of single contractions or sequences of contractions, the latter sometimes summing to produce a sustained declination of the tentacles or contraction in the other parts. Concerts are repeated periodically at intervals of between 1 and 3 min.

Electrical potentials (concert pulses) are recorded from all parts of the body surface at each concert contraction. The potentials are through-conducted at 30–35 cm/sec in parts of the aboral surface. Feeding changes the concert pattern, introducing a type of event called a feeding pulse. Peristalsis in the proboscis, as in *Tubularia*, is exhibited without electrical concomitants.

The observations support the view of *Velella* as a large individual hydroid in no way comparable to a siphonophore. It is regarded as a floating tubularian hydranth with inverted stem. *Velella* and *Porpita* (family Velellidae) are assigned to the superfamily Tubularoidea. The freshwater hydra shows a type of behaviour resembling modified tubularian concerts, and its possible affinity with the tubularoid group is discussed.

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Les chondrophores du genre *Velella* exhibent un comportement de synchronisme semblable et probablement homologue à celui déjà décrit chez *Porpita*, *Pelagohydra* et chez les hydroïdes tubulaires sessiles *Tubularia* et *Corymorpha*. Les mouvements consistent en des flexions des tentacules vers la bouche, accompagnées d'une rétraction des blastostyles et de contractions musculaires du manteau et de la crête surmontant la voile. Les mouvements synchrones peuvent être de simples contractions ou des séquences de contractions dont la sommation produit parfois soit un abaissement soutenu des tentacules, soit une contraction, également soutenue, des autres parties du corps. Les mouvements synchrones se répètent périodiquement à intervalles de 1 à 3 min.

Des potentiels électriques (influx synchrones), détectés dans toutes les parties du corps, accompagnent chaque contraction synchrone. Les potentiels sont transmis par réseau continu aux parties de la face aborale à une vitesse de 30–35 cm/sec. L'absorption de nourriture modifie les caractéristiques de l'influx synchrone et donne naissance à ce qu'on appelle l'influx alimentaire. Comme chez *Tubularia*, les mouvements péristaltiques du proboscis se produisent sans phénomènes électriques concomitants.

Ces observations sont en accord avec le point de vue que *Velella* est un grand hydroïde individual, d'aucune façon comparable à un siphonophore. Nous le considérons comme un hydranthe flottant de tubulaire à tige renversée. Nous assignons *Velella* et *Porpita* (famille des Velellidae) à la super-famille des Tubularoidea. L'hydre d'eau douce a un comportement semblable aux mouvements synchrones des tubulaires. Nous analysons son affiliation possible au groupe des Tubularoidea.

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THE systematic status of *Porpita* and *Velella* has long been debated. These organisms have been regarded as modified medusae, as hydroid colonies related to siphonophores, and as hydroid individuals. Most textbooks still treat them as a subdivision of the order Siphonophora, although modern specialist opinion has moved completely away from this position. *Porpita* and *Velella* are excluded from the order Siphonophora in the two major accounts of that group published in recent years (Totton 1965; Stepan'iants 1967). Most specialists favour a relationship with sessile hydroids rather than with siphonophores. Totton (1954) and Rees (1957) recognized an affinity with athecate hydroids, but assigned *Porpita* and *Velella* to a separate order, Chondrophora. Picard (1955) classified them as a family (Velellidae) within the athecate hydroids having an affinity with *Zanclea* and *Pteroclava* (family Zancleidae, Rees 1957). Brinckmann (1964) also favoured a position in the Athecata but as a superfamily of capitate hydroids with tubularian affinities. In this view she followed Agassiz (1883), Leloup (1929), Garstang (1946), and Mackie (1959, 1960), who on various grounds stressed the tubularian homologies of the chondrophores.

If *Velella* is to be regarded as a hydroid, is it a hydroid individual or is it a colony? Conventionally, it is regarded as a colony, with gastrozooid, gonozooids, and dactylozooids representing individual polypoid types within the colony. Alternatively, it can be regarded as a single large tubularian hydranth. Figure 1 illustrates the latter view. The large central structure bearing the main mouth at its tip is homologized with the proboscis of a sessile hydroid like *Tubularia* or *Corymorpha*, and is thus considered to be part of the primary hydranth rather than being a separate individual, or "gastrozooid." It will here be called the proboscis. The outer fringe of tentacles corresponds to the main (proximal) circle of tentacles in the sessile tubularian, rather than representing dactylozooids. There is no homologue to the small distal tentacles of *Tubularia*. The medusae belong to the Haeckelian family Codonidae, which are characteristic of capitate hydroids, including those tubularians having free medusae.

The structures on which the medusae are borne prior to their release are, in *Porpita* and *Velella*, long mobile appendages with an opening at the tip through which food can be ingested. Adherents to the colonial view argue that these structures are a separate class of polyp individuals, the gonozooids. However, they occupy a position corresponding to that of the blastostyles or racemes of the sessile tubularian, and can be regarded as blastostyles having a secondarily developed oral aperture. This view was adopted by Mackie (1959) and by D. V. Naumov (1961, *cited in* Stepan'iants 1967), who accordingly regard the reproductive appendages not as individuals in a colony but as outgrowths from the hydranth wall of single hydroid individuals.

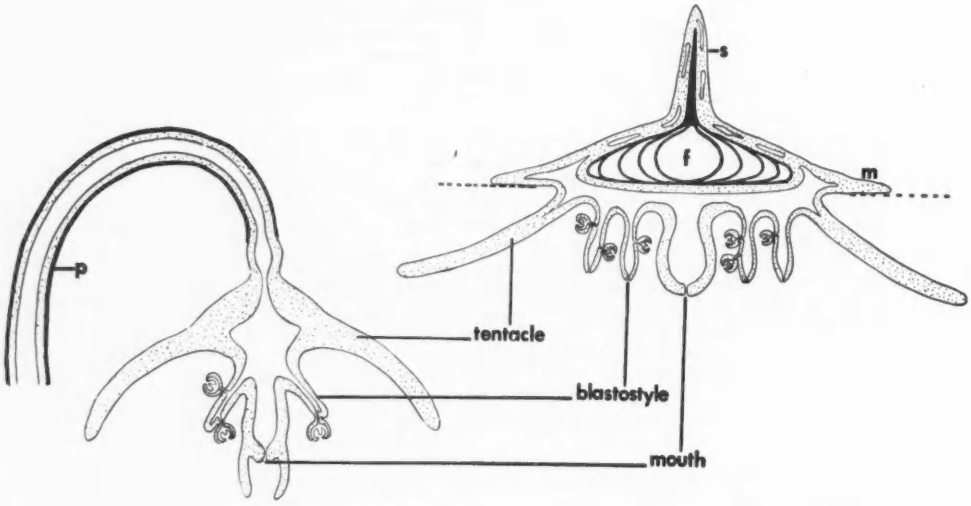

FIG. 1. A chondrophore (*right*) compared with a sessile tubularian hydroid (*left*). For explanation, see text.

Although we accept this view, we should point out that the *Velella* hydranth is a highly specialized one. It floats upside down at the surface instead of sitting on a stalk attached to the bottom. During development, the aboral pole of the larva grows inward forming the first float chamber (Fig. 1, *f*) instead of growing out to form the stem. The invaginated ectoderm layer then secretes a series of secondary float chambers concentric with the first. These layers of chitin presumably correspond to the layers that form the perisarc (Fig. 1, *p*) of the sessile hydroid, but the whole structure is inverted.

Surrounding the hydranth just above the tentacles, an outfolding develops at an early stage. This structure, the mantle, (Fig. 1, *m*) has no homologue in the sessile tubularian. It has a water-repellent upper surface and normally lies flat on the surface film, where it appears to act as a stabilizer.

The aboral sail (Fig. 1, *s*) again has no counterpart in the sessile hydroid. It is set asymmetrically across the top of the float, so that the animal is blown at an angle to the wind and not directly downwind (Mackie 1961; Savilov 1961). In its ability to sail at an angle to the wind and in the existence of mirror-image dimorphism, *Velella* resembles the siphonophore *Physalia*, but these resemblances appear to be entirely convergent, representing independent adaptations to conditions in the rather unusual environment at the air–water interface that they share (Mackie 1961).

Considerable attention has been given to hydroid behaviour in the last decade, with the development of new and specialized electrophysiological recording techniques. We now have detailed records of the electrical concomitants of behaviour in *Hydra* (Passano and McCullough 1964, 1965; Josephson 1967; Rushforth 1967, 1971), *Cordylophora* (Josephson 1961; Mackie 1968), and *Tubularia* (Josephson 1962, 1965; Josephson and Mackie 1965; Josephson and Uhrich 1969). If the chondrophore is indeed a modified individual hydroid, its behaviour should be expected to show resemblances to that of the sessile hydroids to which it is most closely related, and similar electrical patterns should be obtainable in the two instances. A previous study on *Porpita* (Mackie 1959), made before electrical recording techniques had been brought to bear on hydrozoan behaviour, showed apparent behavioural homologies with sessile forms such as *Corymorpha* and gave support to the view that *Porpita* is an individual rather than a colony. We have now observed the behaviour of *Velella* and recorded correlated electrical activity. This new work strengthens the homologies previously proposed.

Materials and Methods

Velella velella L. is abundant in the North Pacific (Savilov 1961) and specimens are frequently washed ashore along the coast from California to northern British Columbia. They occasionally penetrate Juan de Fuca Strait, a major invasion taking place in 1946 when considerable numbers reached Victoria (Carl 1948).

Specimens collected near Sooke, B.C., on April 12, 1970, were placed in glass-covered tanks maintained at 15 C. Since the sails wither in dry air, the humidity of the air beneath the glass was raised by bubbling air through the water in which the animals were floating.

To record electrical events, equipment similar to that used in previous studies on hydroid behaviour was employed (Josephson 1965). In addition to recordings made in the open tanks, recordings were made from specimens in small dishes in a Faraday cage.

On May 7, 1970, some specimens were collected at Asilomar Beach, Pacific Grove, California, and studied at the Hopkins Marine Station, where they were kept in the tanks at 12.4 C. Their activities were recorded on 16-mm movie film. In some sequences, a mirror was arranged to give a simultaneous view of the animals from the side and from below. The films were used in the analysis of behaviour, particularly in the measurement of contraction frequencies. Figure 2 is taken from these movie sequences. Finally, specimens were collected from the open ocean during a cruise on the C.N.A.V. *Laymore* off the Oregon coast, and their behaviour was observed in the laboratory on June 27, 1970.

Results

"Concert" Behaviour

The term "concerts" (Josephson and Mackie 1965) refers to rhythmically occurring events in *Tubularia*, in which the tentacles flex orally in one or a series of synchronized contractions. The term is here applied to similar events in *Velella* and other forms.

In *Velella* concerts, the tentacles flexed orally and, at the same time, the blastostyles shortened symmetrically, and the mantle contracted in the downward (oral) direction. Vogt (1854) observed these movements but did not relate the mantle movements to synchronous events in the tentacles and blastostyles. In some specimens from the *Laymore* cruise, the soft tissues forming the crest on top of the sail contracted in synchrony with the other active parts. At the two ends of the crest, movement was away from the longitudinal axis of the float; thus, the effect of crest contraction was to increase the asymmetry of the sail with respect to the float. Some variation was observed in the intensity with which concert components were expressed in different individuals. Mantle depression was seen only when a portion of the

mantle had fallen below the water surface and was thus free to move (Fig. 2). Normally, with the mantle held flat on the surface, mantle contractions accompanying concerts resulted in no detectable degree of depression.

Concerts consisted of single contractions or sequences of contractions. The contracted parts started to relax immediately following a contraction. In the case of the tentacles, the distance moved in the aboral direction between contractions closely approximated to the distance moved in the oral direction during contractions. In the early stages of a concert sequence, contractions tended to sum and to produce a marked degree of depression of the tentacles. However, an equilibrium point was then reached, with the oral and aboral movements balancing each other. At the close of the sequence, the tentacles and other parts returned to their relaxed positions. The contraction frequency required to maintain the tentacles in a strongly depressed position with the tips curled around under the float as in Fig. 2 was about 1/sec as measured from movie sequences. Frequencies as high as 1.3/sec were observed in one specimen at the height of a concert. In such instances, the to and fro movements of the tentacles were barely discernible, the contractions having assumed a tetanuslike character. Such sustained contractions lasted up to 15 sec. Pulse frequencies in typical concerts showed a pattern of acceleration from a slow start, with some deceleration at the end. These changes in tempo were much less dramatic than those described in *Porpita* (Mackie 1959).

In the specimens examined, not all tentacles took part in concerts. Of those that did, some contracted more strongly than others. As in *Porpita*, a few tended to join in late, after the others had achieved some degree of declination. However, whether they started late or early, or contracted strongly or weakly, all active tentacles showed synchrony during concerts.

Like the tentacles, the blastostyles often reached a tetanic condition, with the component contractions not separately distinguishable to the naked eye. The same was true to a lesser degree for the mantle.

Peristaltic movements were observed in the proboscis, but they showed no temporal relation with concerts. In one specimen showing concerts every 170–190 sec, peristalsis occurred every 34–45 sec.

Concert periodicity in *Velella* varied roughly from 1 to 3 min, but tended to remain fairly constant for any given individual over periods of an hour or more. Concert behaviour was neither induced nor inhibited by photic stimulation. In this respect *Velella* resembles *Tubularia*, but differs from *Pelagohydra* (Pilgrim 1967a, b), which is extremely light-sensitive, responding to a sudden reduction in illumination by vigorous concert activity.

Electrical Correlates of Behaviour

As in *Tubularia*, concerts in *Velella* are accompanied by electrical signals in the millivolt range. They are frequently composite events. The predominant polarity is negative (up) in recordings from the aboral side.

Single oral flexions of the tentacles were accompanied by single pulses, sequential contractions by a series of such pulses (Fig. 3, 4). Not all pulses were accompanied by a visible contraction, especially during concerts of long duration, when the contractions had summed to produce a noticeable degree of declination.

Concert pulses were recorded in some tentacles that were not visibly taking part in the concert, as well as in active ones, but they were recorded at higher amplitudes in the latter (Fig. 5). The pulses were also recorded in the blastostyles, in the proboscis, in the mantle, and all over the aboral surface including the sail and its crest (Fig. 6), and appear to be propagated throughout the whole animal. They appear in different places in slightly different time relations, showing that they are being actively propagated. It is not clear where the pulses originate. Variations in the shape of the pulses recorded at the same point suggest that impulses may be arriving from more than one direction and presumably are therefore being generated at more than one site. Multiple, interacting pacemakers seem to be a fundamental part of the behavioural organization in hydrozoans (Passano 1963).

Electrical stimulation of any of the regions in which concert pulses can be recorded resulted in the generation of propagated pulses similar to spontaneous concert pulses (Fig. 7). Conduction velocities measured in the circular direction on the aboral surface are in the order of 30–35 cm/sec at 15 C.

One specimen of *Velella* was fed on pieces of fish muscle during a long-term recording of its concert activity. The typical electrical activity of this specimen prior to feeding consisted of regular single concert pulses at 75 sec periodicity. For over 15 min following feeding, a new pattern of signals was in evidence (Fig. 8), replacing the former pattern completely for about 11 min, following which the original pattern began to reemerge. Active peristalsis was observed in the proboscis later on, but no electrical events could be associated with this activity, even when electrodes were attached directly

FIG. 2. A *Velella* in the middle of a concert, seen from the side below the waterline. The tentacle tips (*t*) are bent round in the oral direction, most of the blastostyles (*b*) are retracted, and a portion of the mantle (*m*), which has dipped below the surface, has bent in the oral direction.

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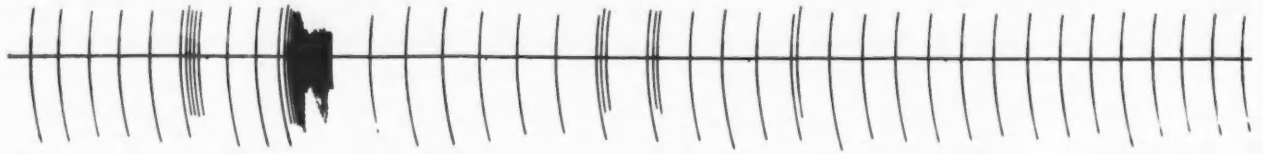

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FIG. 3, 4. Records of concert activity in *Velella* made with a suction electrode attached to the aboral surface while the specimen floated in a container of cooled sea water. (Scales: 5 and 1 min respectively.) The specimen in Fig. 3 showed concerts consisting of single concert pulses roughly every 75–90 sec, with irregular periods of more intensive activity. The specimen in Fig. 4 showed concerts consisting of bursts lasting about 1½ min, each burst consisting of 35–45 pulses.

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to the proboscis. It is not clear if the "feeding pulses" represent events in the system responsible for spreading concert pulses, but stemming from another pacemaker site, or originate in an entirely different conducting system. Mackie (1960) found histological evidence of two superimposed nerve plexuses in *Velella*, but the significance of this double innervation remains unclear.

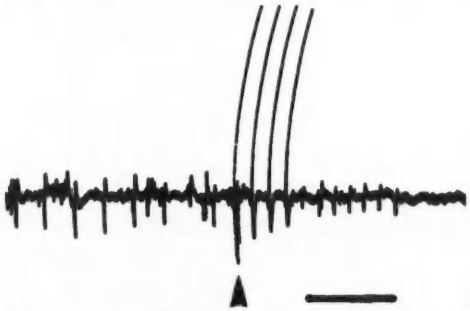

FIG. 5. Record of concert pulses from a tentacle, to show increased amplitude of pulses that occurs when the tentacle begins to flex (*arrowhead*) (scale: 3 sec).

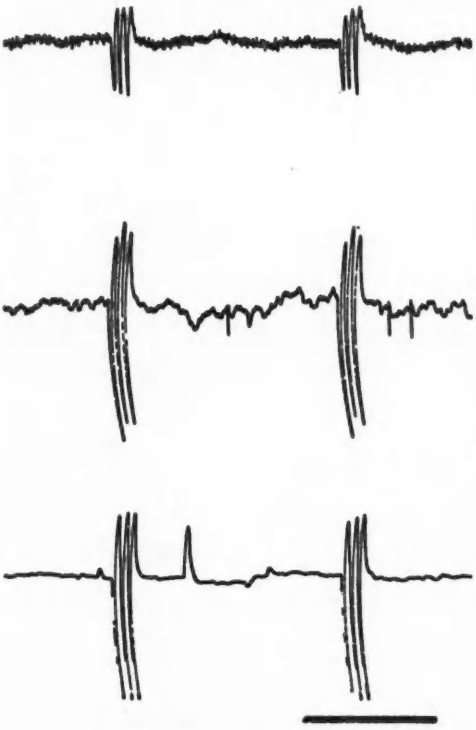

FIG. 6. Three-channel recording from blastostyle (*top*), proboscis (*middle*), and mantle (*bottom*) to show synchrony of composite concert pulses in the three places (scale: 5 sec).

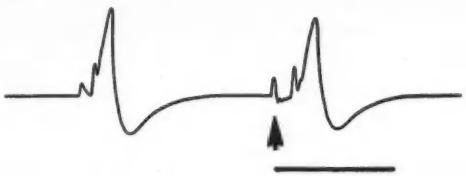

FIG. 7. Following a spontaneous concert pulse, a shock was delivered (*arrowhead*). The induced event resembles the spontaneous one. The recording and stimulating electrodes were both on the aboral surface (scale: 500 msec).

Discussion

The earliest allusion to a tubularian concert that we know of is that of Guilding (1828) for *Porpita* ("... praedam brachiis quibusdam vel omnibus subito declinatis amplectens"). *Porpita* (Mackie 1959), *Tubularia* (Josephson 1962), *Corymorpha* (Parker 1917), and *Pelagohydra* (Pilgrim 1967a, b) show basically similar activities, in which the tentacles are flexed from their normal position by one or a series of contractions to a position where they are more or less gathered in around the mouth. Synchrony of all active components is a general feature, and this has now been demonstrated in *Corymorpha* by E. Ball (unpublished data), a form earlier reported by Wyman (1965) to be exceptional in this regard. Concert periodicities vary in different forms. For example, *Porpita* concerts show a 30-sec periodicity, those of *Tubularia* falling within the range 10 sec to several minutes. In *Tubularia*, the pattern is influenced by nutritional state (Josephson and Mackie 1965). An example of a concert pattern from a recently fed *Tubularia* is shown in Fig. 9 for comparison with the *Velella* records. We lack exact information regarding the influence of nutritional state on the concert pattern in *Velella*, although some short-term effects of feeding have been demonstrated.

Despite variations in concert frequency and pattern, the overall resemblance of concerts in *Velella* and *Porpita* to those in the sessile hydroids is evident. The concert can be regarded as a homologous behaviour pattern within this group of animals. This concept of behavioural homologies between chondrophores and sessile tubularians is fully consistent with the morphological and developmental evidence indicative of close systematic

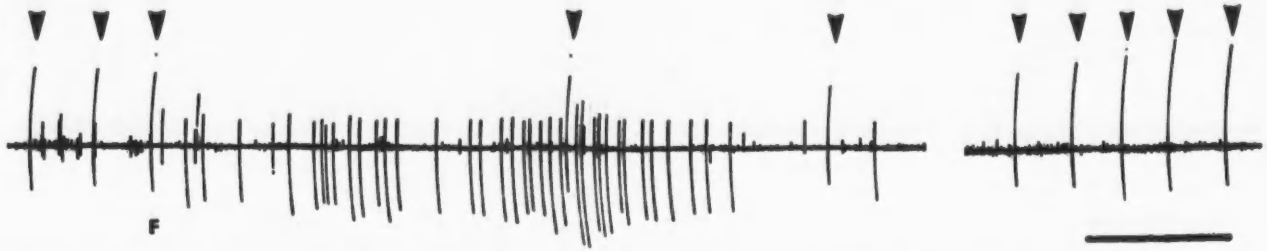

FIG. 8. Following the addition of food at point F, the pattern of concert pulses (*arrowheads*) is interrupted by feeding pulses. The gap in the record represents 8 min, after which the normal concert pattern was again shown (scale: 3 min).

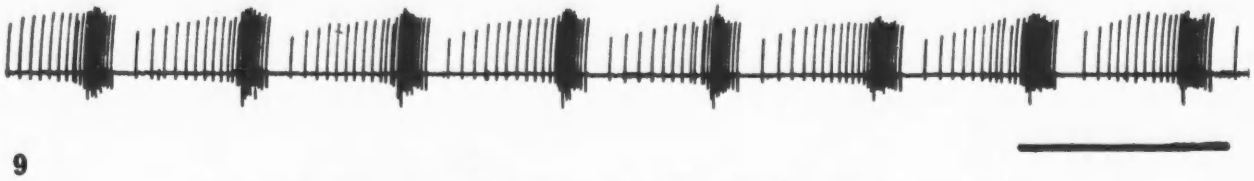

FIG. 9. Concert sequence in *Tubularia* recorded from the neck following feeding (scale: 1 min).

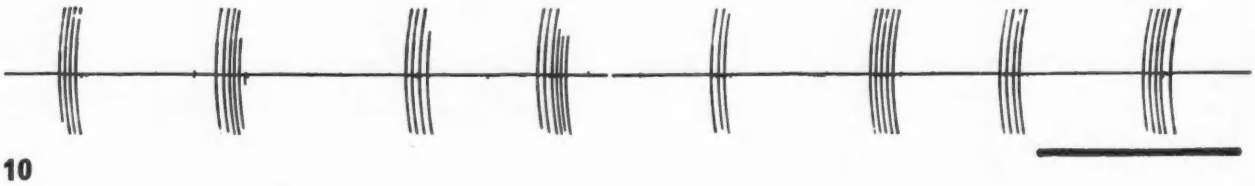

FIG. 10. "Concert" sequence in a fed hydra (contraction burst pattern) (scale: 5 min).

affinity between the two. If a chondrophore is an expanded tubularian hydranth, it would be expected to behave like one. We propose including the chondrophores within Rees' (1957) superfamily Tubularoidea. The classification becomes:

Order ANTHOMEDUSAE

Suborder CAPITATA
Superfamily TUBULAROIDEA
Family Corymorphidae (*Euphysa*, *Corymorpha*, *Branchiocerianthus*, *etc.*)
Family Tubulariidae (*Tubularia*)
Family Margelopsidae (*Margelopsis*, *Pelagohydra*)
Family Velellidae (*Porpita*, *Velella*).

The true siphonophores (order Siphonophora) represent, in our view, a distinct line of evolution characterized by proliferation of polymorphically specialized, secondary polypoids and medusoids from the oozoid, or primary zooid. These complex pelagic bud colonies cannot be accommodated within the Tubularoidea, although their nearest relatives may well lie in that group. Individual gastrozooids and palpons in *Nanomia cara* (a physonectid siphonophore) show behaviour reminiscent of concerts.

The nearest thing to a tubularian concert in any hydroid outside the Tubularoidea is in *Hydra* itself. Dr G. A. Shibley of Lawrence University, Appleton, Wisconsin, has photographed hydras in all stages of their periodic changes in shape. He finds (personal communication) a contraction sequence, involving first the longitudinal muscle of the ectoderm and then the circular muscle of the endoderm of the peduncle, a sequence recalling concerts in *Tubularia* where "neck" contraction corresponds to the second phase in hydra sequence. In both instances the contractions result in displacement of gut fluids toward the anterior end and are followed by downward peristalsis, which redistributes the fluids. Although concerted flexions of the tentacles do not occur in hydra, the contraction sequence otherwise resembles a tubularian concert and has similar electrical correlates. Is hydra descended from tubularian stock? Such a derivation seems preferable to the limnohydrine origins proposed by Bouillon (1968) and Dales (1970). Hydra's possession of stenoteles would seem to link it with capitate hydroids, siphonophores, and chondrophores rather than with the order Limnohydrina, where stenoteles are lacking.

Figure 10 shows a "concert" sequence performed by *Hydra canadensis*, a species that shows concert patterns consisting of one or few pulses, the pattern being influenced by several environmental variables, including feeding stimuli (Rushforth 1971). These pulses accompany the initial contraction phase of the concert. As in *Tubularia* and *Velella*, peristalsis is not accompanied by recordable signals.

The functional significance of concerts is unclear. Several functions may be involved, as several action systems take part. In *Porpita*, the tentacular flexions were reported by Lesson (1843) to function in food collection. In *Velella*, however, the movements are not of sufficient amplitude to be interpretable in this way. In *Corymorpha*, Parker (1917) interpreted concerts as part of a food-collecting cycle, but E. Ball's observations (unpublished data) raise doubts in this regard. In *Tubularia* no food-collecting role has been postulated for the concert flexions.

Some workers have supposed the tentacular flexions to be locomotory, but Mackie (1959) denies any such function in *Porpita*, and Pilgrim's studies (1967a, b) give no support to Dendy's claim (1902) that *Pelagohydra* rows itself through the water by the tentacular flexions. In *Velella*, the movements have no locomotory effect.

In *Tubularia* and *Hydra*, concert movements and accompanying peristalsis combine to bring about trituration of food in the gut and its dispersion. Concerts may have similar effects in *Velella* and *Porpita*, the trituration and dispersion being caused by contraction of the body wall musculature on the oral side, as evinced chiefly in the shortening of the blastostyles, rather than from the tentacular flexions, or contractions in the mantle and sail. These latter movements, like the tentacular flexions in *Tubularia*, would appear to be secondary manifestations, not functional in themselves.

Chun (1897) suggested that the concert movements in *Velella* constituted breathing movements. He envisaged the contractions as compressing the chitinous tracheae that run down from the float chambers into the tissues of the lower side, and as causing air movements within the whole system. The float chambers open to the atmosphere by aboral stigmatal pores. Schneider (1898) criticized this theory, but the matter has not been settled and merits further study. An air-breathing process might be especially useful in *Velella*, where the tissues harbor very large numbers of zooxanthellae.

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Ribonucleotide Reductase in Immature Testes of Salmon

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TARR, H. L. A., AND L. GARDNER. 1971. Ribonucleotide reductase in immature testes of salmon. J. Fish. Res. Bd. Canada 28: 1603–1608.

When cell-free extracts obtained by ultracentrifugation of homogenates of immature salmon testes were incubated with radioactive ribonucleoside di- or triphosphates, the corresponding deoxyribonucleosides were isolated from the reaction mixtures. The specific activities of the crude enzyme extracts were between 15.8 and 54 picomoles of deoxyribonucleoside formed per milligram of protein per hour at 25 C. All attempts to purify the enzyme, which lost activity quite rapidly at 0 C, were unsuccessful. Acid hydrolysis of guanosine deoxyribosides of constant specific radioactivity formed by enzymic reduction of tritiated guanosine triphosphate (GTP) or guanosine diphosphate (GDP) yielded radioactive guanosine of similar specific radioactivity. The crude nature of the preparation, which possessed phosphoribokinase and phosphatase activities, made it impossible to decide whether nucleotide reduction occurred at the mono-, di-, or triphosphate level. Evidence was obtained that allosteric effectors are required for ribonucleotide reduction, as with mammalian and bacterial ribonucleoside diphosphate reductase. The enzyme required dithiothreitol and iron, was strongly stimulated by ethylenediaminetetraacetate (EDTA) and was inhibited by dADP.

TARR, H. L. A., AND L. GARDNER. 1971. Ribonucleotide reductase in immature testes of salmon. J. Fish. Res. Bd. Canada 28: 1603–1608.

L'ultracentrifugation d'homogénats de testicules non-mûrs de saumon a donné un extrait sans cellules qui, après incubation avec des ribonucléosides di- ou triphosphates radioactifs, a permis d'isoler, à même les mélanges de réaction, les désoxyribonucléosides correspondants. L'activité spécifique des extraits enzymatiques bruts se situa entre 15.8 et 54 picomoles de désoxyribonucléoside par milligram de protéine par heure à 25 C. Tous les essais de purification de l'enzyme, qui devint rapidement inactive à 0 C, furent vains. L'hydrolyse acide des désoxyribosides de guanine, de radioactivité spécifique constante et formés par réduction enzymatique de GTP tritié ou de GPD, produisit de la guanine de radioactivité spécifique équivalente. La nature grossière de la préparation, dans laquelle se faisait sentir l'activité des phosphoribokinase et phosphatase, nous a empêché de préciser si la réduction du nucléotide s'effectuait au niveau mono-, di-, ou triphosphate. Nous avons obtenu la preuve que la réduction du ribonucléotide requiert des effecteurs allostériques, tout comme dans le cas de la ribonucléoside diphosphate reductase des mammifères et des bactéries. L'enzyme requiert du dithiothréitol et du fer, et son activité est stimulée par l'EDTA et inhibée par le dADP.

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Specific activities (S.A.) are given as counts/min per μmole of nucleic acid derivative and as picomoles of deoxyribonucleoside formed per hour per milligram of protein at 25 C. Other expressions employed are those tentatively approved by the International Union of Biochemistry. (Biochem. J. 1966, 101: 1–7)

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BERKELEY (1921a, b) was the first to demonstrate that a pentose sugar, presumably D-ribose, is widely distributed in muscles and organs of teleost and elasmobranch fishes, and he concluded that it originated from the mononucleotides of adenine and guanine, which he also found in fish tissues. At that time, knowledge in this field was fragmentary, and it is now practically certain that the compounds he studied arose from acid or alkaline degradation of ribonucleic acid or adenosine triphosphate (ATP). His failure to demonstrate pentose sugar in spring salmon testes was undoubtedly because his analytical method involved formation of furfural from ribose.

The 2-D-deoxyribose in salmon testes DNA yields largely levulinic acid under his assay conditions.

The mechanism of biosynthesis of 2-D-deoxyribose in living organisms remained obscure long after it was identified as the carbohydrate component of DNA by Levene and his collaborators (Levene and London 1929; Levene and Mori 1929). That deoxyribose was formed in consequence of the in vivo reduction of ribonucleotides was suggested by Hammarsten et al. (1950), and this view was supported by the discovery that totally ^{14}C-labeled cytidine was reduced in vivo to deoxycytidine in the rat (Rose and Schweigert 1953). That biosynthesis of deoxyribose usually occurs as a result of enzymic reduction of ribonucleoside diphosphates to the corresponding deoxyribonucleoside diphosphates has now been firmly established, largely as a result of the elegant investigations of Reichard and his collaborators (Reichard 1968; Larsson and Reichard 1967). Reduction of ribonucleoside triphosphates also occurs in certain bacteria as a result of the activity of a different enzyme system (Blakley and Barker 1964; Ghambeer and Barker 1966). Since biosynthesis of DNA proceeds quite rapidly in testes of maturing salmon, and many of the enzymes normally associated with DNA formation, including DNA polymerase, are present in these organs (Tarr 1969; Tarr and Gardner 1971), the possibility that ribonucleoside diphosphate reductase also occurs in them was investigated.

Materials and Methods

Deoxyribonucleoside triphosphates were synthesized as trilithium salts (Smith and Khorana 1963), and other nucleosides, deoxynucleosides, and nucleoside diphosphates were purchased from P. L. Biochemicals. Radioactive ribonucleoside diphosphates were obtained either from New England Nuclear or Schwarz Bioresearch, and dithiothreitol from Calbiochem. The purity of the radioactive compounds was checked by paper chromatography shortly before use. Potato apyrase (Grade I) and *E. coli* alkaline phosphatase (Type III S) were Sigma products.

Immature salmon testes were obtained as in previous work (Tarr and Gardner 1971). Although freshly excised unfrozen testes, and those promptly frozen and stored for 1 or 2 months at –35 C proved satisfactory, prolonged frozen storage in many instances yielded enzyme preparations with little or no activity. Enzyme preparations were made at 0–3 C. In early experiments the testes (usually about 5-g portions) were homogenized briefly in a Serval Omnimix at high speed with 3 volumes of solution containing 5 mM potassium phosphate *p*H 7.2, 5 mM dithiothreitol, 1 mM $MgCl_2$ and 20% glycerol. It was subsequently found that a solution containing only 5 mM $MgCl_2$ and 5 mM dithiothreitol was equally effective.

The homogenates were centrifuged 1 hr at 100,000 *g* and the clear supernatant solutions were used immediately. Several attempts were made to purify the enzyme. Treatment with agents commonly used in enzyme purification, including streptomycin sulphate, alumina C_γ, and spermidine, all markedly reduced activity. Attempts to employ hydroxyapatite columns, which were used with considerable success in partial purification of salmon testes DNA polymerase (Tarr and Gardner 1971), were also unsuccessful. Storage of crude preparations overnight at 0 C usually resulted in considerable, but variable, loss in activity.

Assays for ribonucleotide reductase activity were made under conditions similar to those described by Moore (1967). Reaction mixtures contained 10 μmoles of potassium phosphate *p*H 7.2, 2 μmoles adenosine triphosphate (ATP), 2.5 μmoles magnesium acetate, 2.5 μmoles dithiothreitol, 20 nmoles $FeCl_3$, 0.1 μCi (4.6 nmoles) CDP-2-^{14}C, and enzyme preparation (0.25 ml) in a final volume of 0.5 ml. Values obtained in control assays with enzyme heated 2 min at 100 C were subtracted in all experiments. Reduction of other ribonucleoside diphosphates or triphosphates was carried out under similar conditions, with modifications mentioned in individual experiments.

After 30 or 60 min at 25 C, deoxynucleoside carrier was added (1 μmole dCyd in the case of CDP unless otherwise stated) and the reaction mixtures were heated 2 min in boiling water. The solutions were cooled and the nucleotides dephosphorylated enzymically as described by Moore (1967) except that, in view of the comparatively large amounts of nucleotides present in some experiments, 0.5 mg (0.65 units) of potato apyrase and 5 μliters (0.6 units) of alkaline phosphatase were used, and the incubation periods were extended to 30 min. The enzymes were inactivated by heating as before. The precipitated protein was washed with a little H_2O, and the pooled supernates were assayed.

Where CDP reduction was studied, the solutions were run on to Dowex 1-borate columns and the aqueous effluent that contains all the dCyd but no Cyd was collected (Steeper and Steuart 1970). The first 10 ml of eluate was collected and the radioactivity and dCyd content was determined for calculation of the specific activity. In certain experiments, the dCyd was subjected to paper chromatography to ascertain whether the S.A. was constant.

In experiments where reduction of guanine, adenine, or uridine nucleotides was studied, the above assay was not applicable, and the deproteinized enzyme reaction mixtures were chromatographed directly using an appropriate solvent system and Whatman No. 3MM paper. In these instances, comparatively large amounts of deoxynucleosides were added as carriers, since the chromatographic separations were usually repeated several times in different solvent systems until the compounds attained constant specific radioactivities.

The following solvent systems were used in descending development at 20–22 C using Whatman No. 40 paper, except with the first separations, where 3 MM was used: (A) *n*-propanol, 28% NH_4OH, H_2O; 6:3:1 (Hanes and Isherwood 1949), (B) isopropanol, 28% NH_4OH, H_2O;

7:1:2 (Tener and Khorana 1955), (C) *n*-butanol, 90% HCOOH, H_2O; 77:10:13 (Markham and Smith 1949), (D) 95% ethanol, 1 M ammonium acetate *p*H 7.5 (Palidini and Leloir 1952), (E) *n*-butanol saturated with H_2O (Markham and Smith 1949), (F) *n*-butanol, 95% ethanol, H_2O; 54:32:16 (Putman 1957), and (G) 95% ethanol, 5 M ammonium acetate *p*H 9.5, saturated $Na_2B_4O_7$, 0.5 M ethylenediaminetetraacetate (EDTA); 11:1:4:0.02 (Reichard 1958).

Radioactivities were determined using a Packard Tri-Carb liquid scintillation spectrometer, model No. 3375. Portions (0.5 ml) of aqueous solutions were counted in 10 ml of Bray's solution (1960). Concentrations and purities of eluted nucleosides and related compounds were determined by ultraviolet absorption. Protein was determined by the quantitative biuret reaction, using crystalline bovine albumin as standard (Kingsley 1939). Aqueous solutions of Guo were hydrolyzed 1 hr at 100 C in 0.1 N HCl, and of dGuo for 10 min at 100 C in 0.02 N HCl. For rechromatography, aqueous solutions were concentrated to small volumes using a rotary evaporator at 35 C.

Results

Effect of Substrate Concentration

Standard assays with 0.1 μCi CDP-2-^{14}C were made using 0, 5, 10, and 15 nmoles of nonradioactive CDP and 3 μmoles of dCyd carrier. The deproteinized reaction mixtures were analyzed using Dowex-1-borate columns, and the specific activities of the eluates were determined. The eluates were then subjected to successive paper chromatography using solvent systems A and E. The results (Table 1) show that the S.A. obtained with 5 and 10 nmoles of CDP as substrate were similar, but were lower with 15 nmoles. They also indicate that the radioactivity that is eluted from borate columns, when heated enzyme is used, is not associated with dCyd. Rechromatography indicated that the CdR attained approximately constant S.A.

Table 1. Relation between CDP concentration and the specific activity of the isolated dCyd (0.35 mg protein per assay).

CDP concentration (nmoles)	S.A. of dCyd		
	Eluate from borate column	1st chromatography	2nd chromatography
5 (heated enzyme)		0	0
5 (unheated enzyme)	232	299	325
10 " "	424	260	334
15 " "	120	73	102

The control value of 316 counts/min was subtracted at this stage before calculating the S.A. of the dCyd fractions obtained with unheated enzyme.

Effect of Testes Size, of Frozen Storage, and of Assay Period on the S.A. of Enzyme Preparations

Enzyme preparations were made from testes weighing 9.2 and 13.5 g that had been obtained from different fish and had been frozen and stored 7 days at −35 C. The activity of these two preparations was determined using the standard CDP assay for 30- and 60-min intervals. The results showed that the smaller testis yielded the more active enzyme preparation. In another experiment, a testis weighing 60 g, which had been frozen and stored as above for 8 days, yielded a completely inactive preparation.

Since it proved impossible to obtain a regular supply of unfrozen testes, frozen ones were used in most experiments. However, though extensive experiments were not carried out, it was found that frozen testes that had been stored several months at −35 C usually yielded preparations with quite low activities.

In several experiments, the specific activities of the enzyme preparations were calculated on the basis of the radioactivities of the ribonucleoside diphosphate used and its concentration, and the radioactivity of the isolated deoxyribonucleoside fraction. For five different preparations using the standard CDP assay, the S.A. ranged from 15.8 to 28.0, with an average of 23. In one experiment with UDP-2-^{14}C, the S.A. was 39, and in another with GDP-^{3}H, it was 54. When EDTA or dCDP were added in the standard CDP assay procedure (see below), S.A. of 74 and 73 were obtained.

Assay Conditions

The effect of withdrawal of assay constituents, and of certain additives, on CDP reduction was investigated (Table 2). The enzyme was inactive in absence of dithiothreitol, and its activity was markedly reduced when ATP or FeCl, were not included. Addition of 0.5 mM dADP and dUDP inhibited reduction of CDP, but 1 mM KCN had little effect. Very marked stimulation occurred when 0.1 mM dCDP was present, but when ATP was withdrawn, dCDP alone was not as effective as ATP alone. The addition of EDTA (0.2 mM) caused a threefold increase in rate of CDP reduction. In two separate experiments, 0.1 mM dCTP was used successfully as an effector for CDP reduction,

TABLE 2. Requirements for CDP reduction. Standard assays were carried out for 1 hr at 25 C with 0.41 mg enzyme protein in (*a*) and 0.38 mg in (*b*).

	moles dCyd formed/hr	Inhibition (–), or stimulation (+), (%)
	(*a*)	
No additive	23.2	0
Minus ATP	8.9	–62
Minus $FeCl_2$	15.2	–35
Minus dithiothreitol	0	–100
Plus 1 mM KCN	22.4	–35
Plus 0.5 mM dCDP	57.2	+246
Plus 0.5 mM dCDP, minus ATP	16.5	–29
Plus 0.5 mM dADP	18.4	–19.5
Plus 0.5 mM dUDP	20.6	–11.5
Plus 0.2 mM EDTA	74.0	+314
	(*b*)	
No additive	20.7	0
0.05 mM EDTA	38.8	+39
0.1 mM EDTA	61.0	+195
0.2 mM EDTA	71.5	+246
0.4 mM EDTA	28.7	+42
0.1 mM dCDP	72.0	+248
0.2 mM dCDP	58.0	+180
0.5 mM dCDP	41.0	+98
1.0 mM dCDP	34.6	+67
2.0 mM dCDP	33.7	+63

but it did not enhance the activity of ATP when added simultaneously.

The effect of addition of dCDP and of EDTA on reduction of CDP was investigated. The results (Table 2) show that the optimum concentrations of dCDP and EDTA were 0.1 and 0.2 mM respectively.

REDUCTION OF TRITIATED ATP, GTP, UTP, AND CTP

It has been pointed out by Moore (1967) that ribonucleoside mono-, di-, and triphosphates may be used as substrates in studies of ribonucleotide reduction, in which crude tissue extracts are used as enzyme source, because such extracts often possess mono- and diphosphokinases. Extracts of immature testes of salmon possess such activity and are capable of synthesizing nucleoside di- and triphosphates from the corresponding monophosphates, and also of degrading the polyphosphate esters (Tarr and Roy 1966).

The reduction of the ribonucleoside triphosphates listed in Table 3 was investigated, 5 μmoles of each corresponding deoxyribonucleoside being used as carrier. The products were chromatographed successively using systems G, B, C, and D. The deoxyribonucleosides were then hydrolyzed, and the guanine and adenine separated using solvent system F. The pyrimidine deoxyribonucleosides were further purified in solvent systems C and E. The specific activities of the various compounds were calculated and the results are given in Table 3. In all instances the deoxyribonucleosides attained approximately constant specific activity. The guanine and adenine moieties arising from hydrolysis of the parent deoxyribonucleosides had about the same specific activities. This is to be expected, since separate experiments showed that, in tritiated GTP, 95% of the radioactivity is in the base and only 5% in the ribose.

TABLE 3. Reduction of tritiated ribonucleoside triphosphates. Standard assay conditions were used with an incubation period of 30 min and 0.40 mg protein per assay.

			S.A. of the deoxyribonucleosides and free bases after chromatographic separation in the following solvent systems[a]					
			Deoxyribonucleosides				Adenine	Guanine
Substrate	Amount used (*nmoles*)	Radioactivity (counts/min $\times 10^{-6}$)	C	D	C	E	F	F
ATP	9.2	9.5	1770	1530			1230	
GTP	10.0	6.7	1300	1340				1770
CTP	9.0	3.4	2600	2320	1570	1810		
UTP	11.7	5.5	3860	4180	1770	1570		

[a]The results obtained in the first two chromatographic separations are omitted.

Reduction of Tritiated GDP

Tritiated GDP was reduced under usual assay conditions with 4 mM ATP as effector, and also with 0.2 mM dTTP replacing ATP. The results (Table 4) show that the S.A. of the dGuo fractions, and of the guanine resulting from its hydrolysis, were much higher when dTTP replaced ATP as effector. The fact that the guanine arising from hydrolysis of the dGuo fraction in the heated enzyme experiment possessed no radioactivity shows that the radioactivity of the dGuo fraction in this instance was not associated with the deoxyribonucleoside.

Discussion

Several of the enzyme systems normally associated with DNA formation by the de novo and preformed pathways have now been identified in immature testes of salmon, and have, in some instances, been partially purified (Tarr 1969; Tarr and Gardner 1971). All have proven much more unstable than similar enzymes prepared from mammalian tissues, and the ribonucleotide reductase activity described in the present communication is no exception. The enzyme, which occurred in the cell-free supernatant liquid obtained by ultracentrifugation of homogenates of immature testes, resisted purification by several comparatively mild techniques, including chromatography on hydroxyapatite columns. This fact limited the number of observations that could be made concerning the properties of the enzyme. Since crude extracts of immature salmon testes possess nucleoside mono- and diphosphokinase (Tarr and Roy 1966) and phosphomonesterase (Gardner 1970) activities, it is impossible to state whether the ribonucleotide reductase activity observed in the present study occurred at mono-, di-, or triphosphate level.

Several early attempts in this laboratory to demonstrate ribonucleoside reductase in immature salmon testes failed. It is now realized that this was undoubtedly because the substrates used had comparatively low specific radioactivities. This difficulty was experienced by Reichard (1968) in his early work with an avian reductase system. In the present work between 4 and 40 μmolar substrate concentrations have been used, and about 0.2 μCi of a ^{14}C labeled, or about 5 μCi of a ^{3}H labeled, substrate per assay.

Under these conditions, consistent reduction of ribonucleoside di- and triphosphates has resulted, but the enzyme activities have been low. Thus, with CDP the rate of reduction averaged 23 pmoles per hour per milligram of enzyme protein. In other experiments, values of 39 and 54 were obtained with UDP-2-^{14}C and GDP^{3}H respectively. However, quite low results have also been recorded for crude extracts of mammalian systems. Thus, values of 56 (Fujioka and Silber 1970) and 60 (Steeper and Steuart 1970) have been reported for leukemic mouse spleen extracts, and 113 for a cell-free extract of regenerating rat liver (Larsson 1969). Unlike the salmon testes enzyme, these impure mammalian enzymes were all purified considerably by established techniques.

The allosteric regulation of highly purified ribonucleotide reductase from *E. coli* has been investigated extensively (Reichard 1968; Larsson and Reichard 1967). dTTP is an allosteric effector for both purine and pyrimidine ribonucleoside diphosphates, ATP only for the pyrimidine compounds, and dGTP for the purine compounds. The same general effects have been reported by Moore and Hulbert (1966) for a partially purified nucleotide reductase prepared from Novikoff rat hepatoma. The use of crude extracts that possess phosphokinase and phosphatase activities in the present work has precluded accurate studies of effector requirements. However, it was found that dTTP was a much better effector for GDP reduction than was ATP, and that dCDP greatly enhanced the activity of ATP as effector in reduction of CDP.

The testes enzyme exhibited requirements similar to those of mammalian ribonucleotide reductases. It had an absolute requirement for dithiothreitol, showed only limited activity in absence of an effector such as ATP, and required $FeCl_2$ for optimum

Table 4. Reduction of GDP^{3}H and distribution of radioactivity in the dGuo and G fractions. Reduction of GDP^{3}H (5 nmoles and 5 μCi) was studied in duplicate with addition of 0.2 mM EDTA and 0.38 mg protein per assay. In one instance, 0.2 mM dTTP was used as effector instead of 4 mM ATP. 5 μMoles of dGuo carrier was added to each after 1-hr incubation and the product was isolated by successive chromatography in systems B and C. The guanine resulting from hydrolysis of the dGuo fractions was isolated in system F.

	S.A. of dGuo		
	1st chromatography	2nd chromatography	S.A. of guanine
Heated enzyme	2600	444	0
	2200	475	0
Unheated enzyme	4780	4200	2750
(4 mM ATP effector)	4880	4500	2860
Unheated enzyme	12950	11700	7950
(0.2 mM dTTP effector)	9300	9350	6900

activity. It was inhibited by dADP, strongly stimulated by EDTA, but not affected by KCN. It exhibited marked instability, usually losing about half its activity in 1 day at 0 C.

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Circulatory and Ventilatory Responses of Rainbow Trout (*Salmo gairdneri*) to Artificial Manipulation of Gill Surface Area

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DAVIS, J. C. 1971. Circulatory and ventilatory responses of rainbow trout (*Salmo gairdneri*) to artificial manipulation of gill surface area. J. Fish. Res. Bd. Canada 28: 1609–1614.

Reductions in surface area of the gill were artificially produced by ligating various gill arches and occluding their blood supply. Rainbow trout (*Salmo gairdneri*) responded to a 40–57% reduction in gill area, by increasing cardiac output and ventilation volume, and probably by redistributing blood within the remaining functional gill area. Fish with blood flow to gill arches one and three only, could maintain arterial PO_2 at 90–100 mm Hg, whereas, in those with blood flow to arches three and four only, arterial PO_2 fell to around 40 mm Hg. The presence of a chemoreceptor site for the regulation of arterial PO_2 associated with the efferent blood vessels of arch number one is discussed. Such a receptor may be located in the pseudobranch or in the portion of the brain supplied with arterial blood from the first gill arch.

DAVIS, J. C. 1971. Circulatory and ventilatory responses of rainbow trout (*Salmo gairdneri*) to artificial manipulation of gill surface area. J. Fish. Res. Bd. Canada 28: 1609–1614.

Par le biais de ligature de divers arcs branchiaux et obstruction de leurs vaisseaux sanguins, nous avons artificiellement réduit la surface de la branchie. A une réduction de 40 à 57%, la réaction de la truite arc-en-ciel (*Salmo gairdneri*) a été d'augmenter le rendement cardiaque et le volume d'aération, et probablement aussi de redistribuer le sang sur la surface fonctionnelle de la branchie. Les poissons dont le flot sanguin était dirigé vers les branchies un et trois seulement purent maintenir une pression de PO_2 artériel de 90 à 100 mm. de Hg. Ceux dont le flot sanguin était orienté vers les branchies trois et quatre ont vu leur PO_2 artériel baisser aux environs de 40 mm de Hg. Nous décrivons un site chimiorécepteur associé aux vaisseaux sanguins efférents de l'arc branchial numéro un et capable de régler le PO_2 artériel. Un récepteur de cette nature serait situé dans la pseudo-branchie ou dans cette partie du cerveau qui reçoit le sang artériel du premier arc branchial.

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THE gills of most fish are efficient gas-exchange structures that, in some instances, can remove up to 80% of the oxygen from inspired water (van Dam MS 1938). The volume, distribution, and flow rate of blood passing through the gills will affect the rate of gas transfer between blood and water. Vessels within the gills are arranged in parallel and can be grouped into three categories: the capillaries within the secondary lamellae (lamellar circulation), the blood spaces within the interlamellar region of the filament (lacunar circulation), and the capillaries running within the margin of the filament (filamentar circulation). In vitro observations have demonstrated that distribution of blood flow to different parts of the gill circulation can be altered. In the presence of adrenaline, lamellar blood flow increases whereas acetylcholine enhances filamentar flow (Steen and Kryusse 1964; Richards and Fromm 1969). Richards and Fromm suggested that filamental and lamellar flow is regulated by vasoconstriction and vasodilation of filamental sinus vessels and lamellar arterioles. This mechanism could serve as a means of altering the functional area of the gills. There is considerable in vivo evidence indicating that the functional area of the fish gill is less than its anatomical area and

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that the area may change under certain conditions (Stevens and Randall 1967; Stevens MS 1968; Randall 1970; Davis MS 1971). Thus, different portions of the gill circulation may be perfused at different rates and vascularization of the gills may be adjusted to regulate the functional area of the gills in proportion to the rate of gas transfer.

To study possible variations in functional area of the gills, an experiment was designed to study responses of quiescent rainbow trout (*Salmo gairdneri*) to artificial manipulation of the surface area of their gills. Various gill arches were robbed of their blood supply by ligation, thus reducing the gill area available for exchange. It was hoped that this approach would show how *S. gairdneri* adjusted circulation within the gill and indicate the minimal functional area of the gill required.

Methods

To study trout that had a portion of their gill area removed by ligation, two apparatuses were used. The first consisted of a darkened lucite box similar to the constant flow system of Fry (1957) with a flow of water through it (200–250 ml/min) and a partition to prevent the fish turning around. Twenty-one fish (218 ± 8 g, 12.0 ± 0.2 C), ligated in various ways and equipped with dorsal aortic cannulae to sample blood for arterial PO_2 determinations (Smith and Bell 1964), were placed individually in the box. The appropriate gill arches were tied off at their bases, close to the isthmus, by means of two number "0" silk ligatures tightly applied. In one individual the gill blood supply was not disturbed but the right operculum was tied shut. Each fish partially recovered on the operating table and was then placed in the experimental box for overnight recovery. On the following day at intervals over a 6–8-hr period, PaO_2[1] data were obtained along with values for PIO_2 and PEO_2. From these data, and with values for $\dot{V}G$ (see below), the oxygen uptake rate ($\dot{V}O_2$) was calculated by the Fick principle:

$$\dot{V}O_2 = \dot{V}G\ (PIO_2 - PEO_2) \propto WO_2$$

where $\dot{V}O_2$ = the oxygen uptake rate in ml/min per fish; $\dot{V}G$ = the ventilation volume in ml/min per fish; PIO_2 = inspired oxygen tension, mm Hg; PEO_2 = expired oxygen tension, mm Hg; $\propto WO_2$ = the oxygen solubility coefficient in water at the test temperature (ml O_2/ml per mm Hg).

Oxygen tensions were measured with a Radiometer Copenhagen oxygen electrode in a thermostatted microcuvette and a Radiometer PHM-71 acid–base analyser as described by Cameron and Davis (1970) and Davis and Cameron (1971).

Cardiac output, $\dot{Q}$, was also calculated by the Fick principle (Davis and Cameron 1971) using the measured PaO_2, blood curves for rainbow trout at the test temperature, and a PCO_2 of 1–2 mm Hg (Cameron 1971), the relation betwwen hematocrit and blood oxygen content of Holeton and Randall (1967):

$$\propto BO_2 = 0.311\ HCT + 0.7$$

and an assumed $P_{\bar{v}O_2}$ of 30 mm Hg. This assumption is probably justified, as the results of Cameron and Davis (1970), Davis and Cameron (1971), and Holeton and Randall (1967) all indicate that $P_{\bar{v}O_2}$ in rainbow trout remains steady at 30–35 mm Hg.

Ventilatory responses of ligated fish were studied using the oral membrane technique described by Davis and Cameron (1971). In this procedure a rubber membrane is stitched to the margin of the mouth and the fish is placed in a lucite $\dot{V}G$ measurement box. The membrane separates inspired and expired water and allows collection of the latter for direct determination of ventilation volume. Nine trout (217 ± 8 g, 11.7 ± 0.5 C) were ligated and equipped with oral membranes. Each fish was then placed in the $\dot{V}G$ measurement box for overnight recovery. The following day $\dot{V}G$, PIO_2, and PEO_2, and ventilation rate (VR — breathing movements/min) were recorded at intervals over an 8-hr period as described by Davis and Cameron (1971). $\dot{V}O_2$ was calculated as previously described, and ventilatory stroke volume, the water pumped over the gills/breathing cycle (Vsv), was calculated by dividing $\dot{V}G$ by VR. Utilization of oxygen from the inspired water, expressed as a percentage (% U), was calculated from:

$$\%U = \frac{PIO_2 - PEO_2}{PIO_2} \times 100$$

The blood supply to the gill arches was occluded by ligatures at the base of arches 1–4, numbering the arches from anterior to posterior. A number of patterns of ligation were used and in some instances involved a considerable reduction of gill surface area. Hughes (in Paling 1968) gave the following figures for the gill surface area of a single 175-g brown trout (*Salmo trutta*):

Pairs of gills	Surface area, mm^2
1st	16364
2nd	17422
3rd	15254
4th	10164
	59204

These figures could be used to calculate the percentage of total gill area removed by ligation of various arches

[1]Explanation of symbols used: *Primary characters* — P, partial pressure of gas in mm Hg; $\dot{V}$, volume flow per unit time; $\dot{Q}$, cardiac output per unit time; Vsv, ventilatory stroke volume per breathing cycle; VR, ventilation rate; % U, percent utilization; HCT, hematocrit or packed cell volume in percent; $\propto$ B, solubility coefficient for gas in blood; $\propto$ W, solubility coefficient for a gas in water. *Secondary characters* — *a*, arterial; *v*, venous; I, inspired; E, expired; CO_2, O_2, molecular species; G, referring to the gills.

or groups of arches. It was felt that such calculations would be reasonably accurate as Hughes' data was for fish of similar species and size to those used in the present study. To insure that a particular ligation was successful, the fish were killed after the experiment and the gills were examined. Arches that were successfully ligated appeared dark and contained hemorrhagic spots in the lamellae. When the first arch was tied off, the pseudobranch on that side also appeared dark and necrotic on postmortem examination. The pattern of ligations used is summarized in Table 1.

Results

Cardiovascular and respiratory parameters for nonligated and ligated fish in the flow-through boxes are given in Table 1. Arterial PO_2 in the control group was 100.2 ± 4.1 mm Hg and remained high as long as the blood supply to arch number 1 was intact, even when 40% of the total gill surface area was removed by ligation of arches 2 and 4 on both sides. When arch 1 was ligated on both sides, PaO_2 dropped to 56.8 ± 7.9 mm Hg following only a 28% reduction in gill area, and when arches 1 and 2 were tied off on both sides, reducing the gill area by 57%, mean PaO_2 dropped to 40.3 ± 5.2 mm Hg. As large areas were removed, $\dot{V}O_2$ rose and the magnitude of the rise was most dramatic in fish with four arches removed and the blood supply to arch 1 intact.

Cardiac output, calculated by the Fick principle using an assumed venous oxygen and carbon dioxide tension of 30 and 2–3 mm Hg respectively, rose when gill area was reduced 38–40% (Table 1). $\dot{Q}$ values for fish with arch 1 ligated on both sides may be suspect as PaO_2 fell in those individuals. With such a fall in arterial oxygen tension, venous PO_2 may have fallen also, and the magnitude of this decline and its effect on Fick calculation of $\dot{Q}$ would therefore not be known. In fish with arch number 1 intact and four arches removed, calculated $\dot{Q}$ rose to 24 ± 2.4 ml/min, roughly a fourfold increase over the cardiac output of the nonligated control group.

The results of the ventilation study on ligated and nonligated fish are given in Table 2. The group with four arches ligated and arch number 1 intact had $\dot{V}G$'s that were about three times higher than the nonligated group. In addition, percent utilization of oxygen fell from 46 to 27% but $\bar{x}$ $\dot{V}O_2$ was 41% higher than the nonligated group. The group that had four arches ligated and the blood supply to arch 1 destroyed on both sides had a $\bar{x}$ $\dot{V}G$ slightly over twice that of the nonligated group and a $\bar{x}$ $\dot{V}O_2$ 30% higher. Thus, the group with arch 1 blood supply intact showed a larger $\dot{V}G$ and $\dot{V}O_2$ increase in comparison to the controls than did the group with arch 1 ligated.

Discussion

Oxygen uptake rate, ventilation volume, and calculated cardiac output all increased in response to removal of portions of the gill by ligation of its blood supply. Thus, the fish responded by increasing the volume flow of both water and blood past the exchange surface. As ventilation volume increased, percent utilization decreased, likely as a result of the elevated water flow through the gill sieve (van Dam MS 1938).

Gill area in resting trout can be reduced by 40% and the fish can still maintain full oxygen saturation of arterial blood and double $\dot{V}O_2$. Thus, adequate

TABLE 1. Cardiovascular and respiratory parameters (mean ± SE; number in parentheses) for nonligated and ligated rainbow trout held in flow-through boxes.

% gill removed	Ligations	Arch 1 blood supply	No. fish used	PaO_2 *mm Hg*	$\dot{V}O_2$ *mg/kg per hr*	$\dot{Q}$ *ml/min*	HCT *vol %*
0	None — controls	Intact	4	100.2±4.1(17)	44.9±0.1(19)	6.2±1.2(17)	17.2±2.6(5)
14	Arch 1 on right side	Intact on left side	1	110±10.6(3)	24.7±0.8(5)	0.96±0.3(3)	28.0(1)
28	Arch 1 both sides	Destroyed	4	56.8±7.9(11)	49.2±0.7(17)	19.6±9.4(9)	20.8±3.5(3)
57	Arches 1 and 2 both sides	Destroyed	5	40.3±5.2(18)	60.5±0.6(19)	20.2±5.0(12)	23.5±2.4(6)
38	Arches 2 and 4 right, 2 left	Intact	2	90.9±3.4(8)	67.3±0.4(8)	21.3±1.3(8)	19.5(2)
40	Arches 2 and 4 both sides	Intact	4	87.9±3.5(12)	90.8±0.8(16)	24.0±2.4(12)	23.3±4.5(3)
0	None — right operculum sewed shut	Intact	1	112.0±1.0(3)	68.1±0.7(5)	6.1±1.1(3)	31.0(1)

TABLE 2. Ventillatory data (mean ± SE; number in parentheses) from nonligated and ligated rainbow trout in the $\dot{V}G$ measurement box with oral membranes attached.

% gill removed	Ligations	Arch 1 blood supply	No. fish used	$\dot{V}G$ *ml/min*	VR *no./min*	Vsv *ml/breath*	U %	$\dot{V}O_2$ *mg/kg per hr*	Temp *C*
0	None — controls	Intact[a]	18	37.0±1.8(18)	73.8±3.4(18)	0.5±0.02(18)	46.0±1.5(18)	55.3±2.1(18)	8.6±0.2(18)
57	Arches 1 and 2 both sides	Destroyed	5	83.3±6.5(43)	93.8±1.4(42)	0.9±0.1(41)	34.1±2.1(21)	71.9±0.5(21)	11.6±0.03(5)
40	Arches 2 and 4 both sides	Intact	4	115.6±9.7(34)	97.9±0.6(33)	1.2±0.1(33)	27.0±1.8(25)	77.9±0.5(25)	11.8±0.08(4)

[a]Values for controls are grand means calculated from individual means for each fish (total number of observations > 200).

gas transfer can be maintained even if the functional area of the gill is much less than the anatomical area.

Ability to maintain high arterial PO_2's appeared to be related to the integrity of blood flow to the first gill arch. If there was no flow of blood to this arch, arterial oxygen tension was low, even though only 28% of the gill area had been removed by ligation of two arches (Table 1). Thus, with the first gill arch destroyed and only 28% of the gill surface area removed, the arterial PO_2 dropped to a greater degree than when 38 and 40% of the gill area was removed but the first arch left intact. The low arterial PO_2's in fish with arch 1 ligated could be explained in part by the ventilation study results (Table 2). These fish did not elevate $\dot{V}G$ and Vsv to the same extent as fish with intact arch 1 circulation. Low PaO_2's could thus have resulted from insufficient ventilatory flow to counteract the reduced gill surface area and metabolic demands associated with the stress of ligation.

What is unique about the distribution of blood to arch 1? These results could be explained if this arch were the site of a large portion of the gaseous exchange in these fish. Thus, if arch 1 were removed, a drop in arterial tension would result. Such a possibility seems unlikely, and infrared photographs of the whole gill on one side taken when a portion of the operculum was removed show no special blood distribution to arch 1 (J. C. Davis unpublished data). A more plausible explanation may relate to the location of the pseudobranch. Laurent (1967) and Laurent and Rouzeau (1971) have found evidence for chemoreceptor and baroreceptor activity in the pseudobranch. The pseudobranch receives its blood supply from an extension of the first efferent artery (Laurent and Dunel 1966). Ligation of arch 1 on both sides would rob both pseudobranchs of their blood supply and lead to degeneration. Those fish with arch 1 ligated had no functional pseudobranch and were unable to maintain arterial PO_2 levels in the face of reduced gill surface area. Thus, the pseudobranch may well serve as an important site in the regulation of arterial oxygen tension.

It is possible that ligation of arch 1 could affect other vital centres not located in the pseudobranch. Blood flow to a portion of the brain served by a branch of the efferent branchial artery from arch 1 could have been disrupted. Alternatively, destruction of the pseudobranch may have caused severe stress and disability and led to a generalized inability of the fish to respond to reduced gill area.

The fish with intact gill circulation, but the right operculum sewed shut, was able to maintain PaO_2 at saturation level but appeared to be breathing hard. This animal had an oxygen uptake rate about 50% above that of the undisturbed controls, but its calculated $\dot{Q}$ did not appear to be different from that of the controls (probably because this fish had such a high hematocrit — Table 2). It appeared that this fish could maintain effective gas exchange in the face of a poor pattern of water flow to one side of the gills but that considerable energy expenditure was required for it to do so. Perhaps this fish utilized a redistribution of blood within the portion of the gill receiving water and thus achieved a better ventilation–perfusion relation in the portion of the gill that was flushed with water.

It appears that rainbow trout can survive a considerable reduction in gill surface area, providing the blood supply to the first gill arch on both sides is intact. This suggests that the remaining gill area is sufficient to meet gas exchange requirements and that the entire gill surface may not be used during normal respiration in quiescent, nonligated trout. Indeed, a mechanism for blood redistribution within the gill, such as that suggested by Richards and Fromm (1969) may be important in permitting the trout to survive reductions in gill surface area. Such a system, together with a regulated flow of water and blood past the gills, likely provides trout with an efficient means of controlling the passage of substances across the respiratory epithelium.

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Eualus berkeleyorum n.sp., and Records of Other Caridean Shrimps (Order Decapoda) from British Columbia

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BUTLER, T. H. 1971. *Eualus berkeleyorum* n.sp., and records of other caridean shrimps (order Decapoda) from British Columbia. J. Fish. Res. Bd. Canada 28: 1615–1620.

A new shrimp species *Eualus berkeleyorum* (family Hippolytidae) is described. The first known occurrence off British Columbia of four pelagic species are recorded: *Parapasiphaë sulcatifrons* Smith (family Pasiphaeidae); *Acanthephyra curtirostris* Wood-Mason, *A. quadrispinosa* Kemp, and *Systellaspis braueri* (Balss) (family Oplophoridae).

BUTLER, T. H. 1971. *Eualus berkeleyorum* n.sp., and records of other caridean shrimps (order Decapoda) from British Columbia. J. Fish. Res. Bd. Canada 28: 1615–1620.

L'auteur décrit une nouvelle espèce de crevette, *Eualus berkeleyorum* (famille Hippolytidae). Il mentionne pour la première fois la présence de quatre espèces pélagiennes au large de la Colombie britannique: *Parapasiphaë sulcatifrons* Smith (famille Pasiphaeidae); *Acanthephyra curtirostris* Wood-Mason, *A. quadrispinosa* Kemp et *Systellaspis braueri* (Balss) (famille Oplophoridae).

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DURING the course of surveys by this station's vessels between 1963 and 1969, a large and varied collection of shrimps was obtained. Examination of the material has led to the preparation of this paper, which aims to describe a new species, *Eualus berkeleyorum*, and to record the first known occurrences in the British Columbian marine environment of four bathypelagic species: *Parapasiphaë sulcatifrons*, *Acanthephyra curtirostris*, *A. quadrispinosa*, and *Systellaspis braueri*. Each of the four bathypelagic shrimps has a cosmopolitan distribution, normally occurring in low latitudes. *Acanthephyra quadrispinosa* was collected in the western Pacific Ocean (37°08′–45°07′N, 146°11′–162°53′E) during the first trans-Pacific cruise of the Canadian research vessel *Endeavour* in March and April 1969 (Anon. MS 1970). The other three species have been caught previously off the Oregon coast (Pearcy and Forss 1966).

In 1964 and 1968, the *G. B. Reed*, equipped with Agassiz and shrimp otter trawls and a "triangle" dredge[1], was employed for fishing in deep water adjacent to the west coast of Vancouver Island (Bernard et al. MS 1967, MS 1970). The same vessel, in 1964, carried out midwater trawling near the Queen Charlotte Islands, B.C. (Taylor MS 1967, 1968). Two smaller vessels, *A. P. Knight* and *Investigator No. 1*, each equipped with a shrimp otter trawl, made five cruises, yielding shrimp material of interest in the Strait of Georgia and Chatham Sound from 1963 to 1969.

I am privileged on this occasion to name the new species as a tribute to Cyril and the late Edith Berkeley. I personally owe much to both for help and inspiration.

Abbreviations used here are: c.l. for carapace length, from the eye orbit to the posterior mid-dorsal edge; and t.l. for total length, from tip of rostrum to tip of telson.

Family PASIPHAEIDAE

Parasiphaë sulcatifrons Smith 1884

Distribution — North Atlantic Ocean, West Africa, Indian Ocean, North Pacific Ocean to Queen Charlotte Sound, B.C.; 500–5400 m.

Present collection — 35 miles S × W Cape St. James (51°26′N, 131°09′W), June 15, 1964; *G. B. Reed* station 64-6-21; daytime, horizontal tow between 640 and 730 m

[1]Having a triangular frame of heavy iron, each side 40 inches (102 cm), with attached bag of ¾-inch (19-mm) mesh.

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with a large nonclosing Engel midwater trawl[2]. One male, c.l. 22.1 mm, total length unobtainable due to damaged telson.

Remarks — The paper by Sivertsen and Holthuis (1956) has been consulted for the previously known range of the species. The present specimen fits the description by Chace (1940) very closely.

Family OPLOPHORIDAE

Acanthephyra curtirostris Wood-Mason 1891

Distribution — Caribbean region of Atlantic Ocean, east coast of Africa, Indo-Pacific region to Japan and the Hawaiian Islands, west coasts of North and South America, Peru to Vancouver Island, B.C.; 200–5000 m.

Present collection — 67 miles WSW of Cape Scott, Vancouver Island (50°56.4′N, 130°12.2′W), maximum depth 2178 m, September 11, 1964; *G. B. Reed* station 64-212; daytime tow on the bottom with shrimp otter trawl[3]. One male, c.l. 16.3 mm, total length unobtainable due to damaged rostrum; rostral spines, 8/1.

Remarks — The general distribution was summarized from earlier published records (Chace 1937, 1940; Pearcy and Forss 1966). It is not unlikely that the specimen was captured while the trawl was being returned to the surface, and the same could apply to other records of oplophorids here.

Acanthephyra quadrispinosa Kemp 1939

Distribution — South Atlantic Ocean, Indian Ocean, Indo-Pacific region, North Pacific Ocean to the open ocean off Japan, and Vancouver Island, B.C.; vertical distribution uncertain.

Present collection — *G. B. Reed* station 64-212 (details above). One female, c.l. 17.7 mm, t.l. 83 mm; rostral spines 12/4.

Remarks — Earlier records of the distribution of the species were taken from Kemp (1939). The tips of both branchiostegal spines are broken off but enough of the flared supporting carinae remain to permit, along with other characters, a definite identification.

[2]This net was 1200 20-cm meshes (stretched measure) in circumference, and graded through a series of mesh sizes to 2 cm in the codend.

[3]The so-called Gulf of Mexico flat trawl, having headrope and footrope each 40 ft (12.2 m) in length, and a mesh size throughout of 38 mm.

Systellaspsis braueri (Balss 1914)

Distribution — Atlantic Ocean, Bermuda to Georges Bank and Gulf of Guinea to Scotland; Indian Ocean; northeastern Pacific Ocean, Los Angeles to Vancouver Island; within 150 m of the surface and to 4000 m.

Present collection — 35 miles W × N of Estevan Point, Vancouver Island (49°19.0′N, 127°26.6′W), 1460 m. September 9, 1964; *G. B. Reed* station 64-197; daytime tow on the bottom with shrimp otter trawl. One male; c.l. 27.1 mm, t.l. 110 mm, rostral spines 12/2. *G. B. Reed* station 64-212 (details above). Three females; one, c.l. 15.6 mm and t.l. 67 mm; others, c.l. 14.8 and 20.3 mm, total lengths unobtainable due to damaged telsons and rostrum; rostral spines 9–12/2–3.

Remarks — According to Chace (1940), and Sivertsen and Holthuis (1956), this species is quite rare.

Family HIPPOLYTIDAE

Eualus berkeleyorum n.sp.

Material examined — All 15 specimens examined were females. Table 1 lists details of capture and carapace lengths.

Description — Body moderately slender, little compressed. Integument thin, smooth. Rostrum fairly short, about 0.4 times carapace length, not reaching second segment of antennular peduncle; descending; upper limb wider than lower; spines 8–11/2–5, dorsal spines all much same size, closely and evenly spaced giving a serrated appearance, and larger than ventral; tip normally acute, rarely bifid or trifid. Carapace about 0.25 times total length; anterior high in profile (Fig. 1), and frontal margin rather sinuous (Fig. 2*f*).

Carapace spines: suborbital strong, pointed and slightly ascending; antennal strong with supporting carina; pterygostomian small, yet conspicuous.

Eye moderate in size, including cornea. Antennule: peduncle moderately long, second segment longer than third; stylocerite strong and almost reaching end of basal segment; inner (lower) flagellum slightly longer than outer, both extending far beyond end of scaphocerite.

Antenna: scaphocerite oblong, lamella exceeding spine (Fig. 2*b*); flagellum exceeds total length. Mandible: palp of two segments, incisor process having 3 teeth; molar process with large irregular surface (Fig. 2*a*). Third maxilliped: stout, extending considerably beyond scaphocerite; having about 10 spines on distal end (Fig. 2*c*); with epipod, and long exopod. Pereiopods: I, stout, shorter than third maxilliped, all segments much same length, chelate (Fig. 2*d*), with epipod; II, slender, about 1.5 times length of I, carpus with 7 segments, chelate, with epipod; III, slender, merus armed with 4 strong spines, dactylus slender and slightly curved, with epipod; IV, slender, merus with 5 spines, dactylus as in III; V, slender, merus having 1 or 2 spines, dactylus as in IV; III–V, all about equal in length, and longer than II.

TABLE 1. *Eualus berkeleyorum* n.sp. Material examined.

Vessel	Locality	Geographic location	Depth (*fath*)	Depth (*m*)	Gear	Date	No. female specimens	Carapace length (*mm*)
Investigator No. 1	Off Gabriola Is., Strait of Georgia	49°09.0'N 123 32.6 W	210	384	Shrimp otter trawl	Dec. 3, 1963	4	6.8, 8.8[a], 9.5, 9.8
"	Off Bowen Is., Strait of Georgia	49 18.4 N 123 30.7 W	88–89	161–163	"	Dec. 11, 1963	2	7.4, 7.6
"	Off Denman Is., Strait of Georgia	49 36.6 N 124 46.6 W	50	91	"	Oct. 25, 1968	1	5.8
"	Off Comox Bar, Strait of Georgia	49 38.6 N 124 48.8 W	48–49	88–90	"	May 22, 1969	1	6.9
"	Off Comox Bar, Strait of Georgia	49 39.1 N 124 49.8 W	40	73	"	May 23, 1969	1	5.0
A. P. Knight	Off Greentop Is., Chatham Sound	54 11 N 130 28 W	50	91	"	Aug. 3, 1964	1	7.1
A. P. Knight	Off South Rachael Is., Chatham Sound	54 10 N 130 32 W	58	106	"	Aug. 3, 1964	3	6.5, 7.2, 7.6
G. B. Reed	Off La Pérouse Bank, west coast of Vancouver Is.	48 47.0 N 126 31.0 W (station 68–47)	156	285	Agassiz trawl	Sept. 11, 1968	1	8.6
G. B. Reed	Off La Pérouse Bank, west coast of Vancouver Is.	48 53.0 N 126 20.2 W (station 68–49)	86	158	Triangle dredge	Sept. 11, 1968	1	7.3

[a]Holotype.

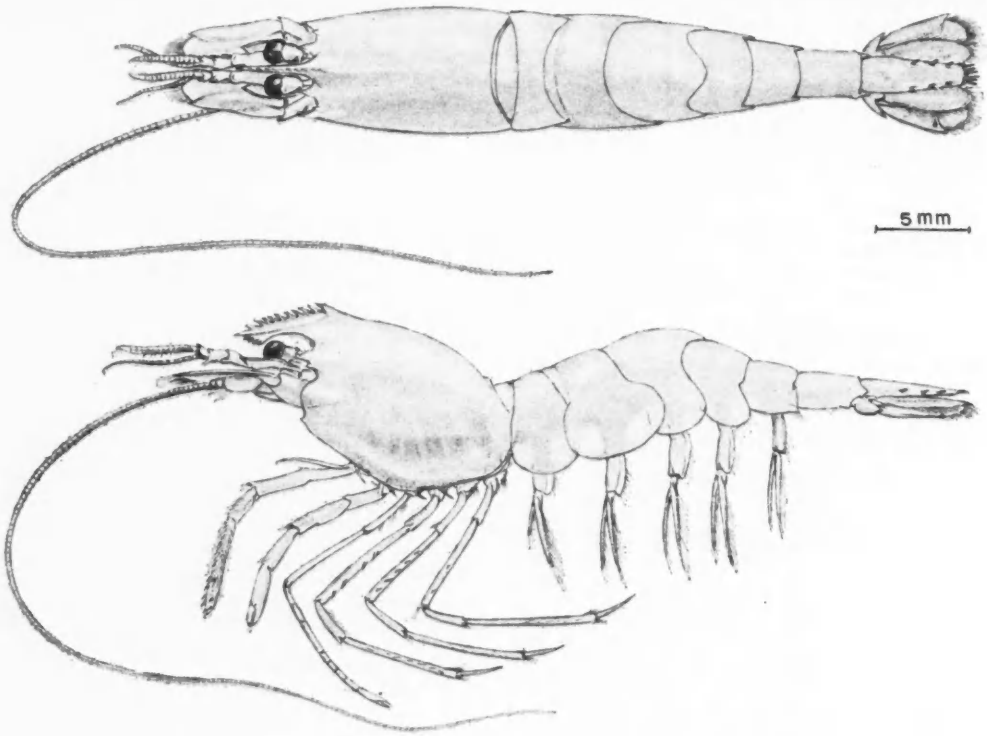

FIG. 1. *Eualus berkeleyorum* n.sp. Dorsal and lateral views of female.

Abdomen: median dorsal margin of third somite strongly produced posteriorly; fifth somite with small recessed spine on postero-lateral margin; pleura of first to fourth somites rounded, fifth with postero-ventral portion projected; sixth somite somewhat longer than fifth, and shorter than telson. Telson with 3 pairs of lateral spines, and posterior margin broadly rounded, almost truncate, bearing 3 pairs of spines that decrease slightly in length from the inner to outer pair. Inner uropod longer than outer, and both extend beyond telson (Fig. 2*e*).

Colour: background white to cream; red to orange patches on rostrum, frontal, branchial, and postero-dorsal margins of carapace; also on peduncle of antenna, third maxillipeds, and first pereiopod; and saddlelike bands of the same colour on the abdominal somites.

Size: carapace lengths of females 5.0–9.8 mm; total lengths 23–38 mm.

Range and habitat — British Columbia coast, Vancouver Island to Chatham Sound; 73–384 m (40–210 fath). One specimen (*G. B. Reed* station 68-47) was captured on a rock and sand bottom, and all others on soft mud. There is a tendency (Table 1) for larger individuals to inhabit deeper water.

Types — The holotype is a female, c.l. 8.8 mm, and t.l. 34 mm, collected in the Strait of Georgia (49°09.0′N, 123°32.6′W). It is deposited in the National Museum of Canada (NMC 15316) with one paratype (NMC 15317). The U.S. National Museum, Washington, D.C., and the Rijksmuseum van Natuurlijke Historie, Leiden, have specimens.

Remarks — The new species belongs to the genus *Eualus* Thallwitz, 1892, with its main characters: the carpus of the second pereiopod with seven segments; exopod on the third maxilliped; and a mandibular palp of two segments (Holthuis 1947). Within the genus, it fits with *E. avinus* (Rathbun 1899), *E. pusiolus* (Krøyer 1841), and *E. herdmani* (Walker 1898) into a group having in common epipods on the first three pereiopods and a relatively short rostrum. *Eualus berkeleyorum* differs from the others by the descending rostrum with eight or more

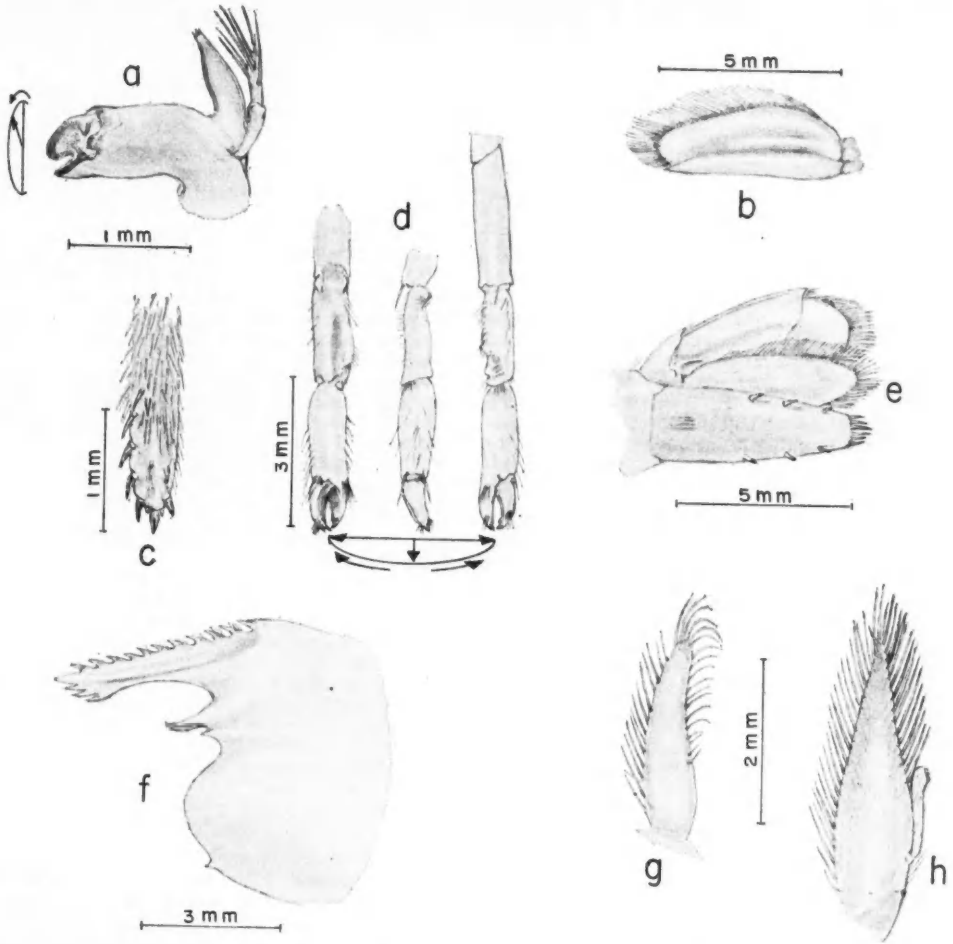

FIG. 2. *Eualus berkeleyorum* n.sp. Parts of female: (*a*) mandible; (*b*) scaphocerite; (*c*) distal end of third maxilliped; (*d*) first pereiopod; (*e*) tail fan; (*f*) anterior portion of carapace; (*g*) endopod of first pleopod; (*h*) endopod of second pleopod.

closely spaced dorsal teeth; telson with the distal end broadly rounded; absence of a spine on the pleuron of the fourth abdominal somite. Another, even more, unique character is the sinuous frontal margin of the carapace in *E. berkeleyorum*.

One specimen, c.l. 5.0 mm, from near Comox Bar, 73 m (Table 1), was parasitized by the abdominal bopyrid isopod, *Hemiarthrus abdominalis* (Krøyer).

Another female, c.l. 6.9 mm, from the same locality, captured on May 22, 1969, had a few eyed eggs attached to pleopods.

Acknowledgments

I am indebted to Mr A. A. Denbigh of this station for the excellent illustrations. Specimens of *Acanthephyra quadrispinosa*, collected during the first Canadian trans-Pacific oceanographic cruise, were identified by Mr

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Taxonomy, Distribution, and Biology of the Northern Rockfish, *Sebastes polyspinis*

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WESTRHEIM, S. J., AND H. TSUYUKI. 1971. Taxonomy, distribution, and biology of the northern rockfish, *Sebastes polyspinis*. J. Fish. Res. Bd. Canada 28: 1621–1627.

Available information is summarized on the taxonomy, distribution, abundance, and biology of the northern rockfish, *Sebastes polyspinis* (Taranetz and Moiseev 1933). Morphological and biochemical descriptions of the taxon are provided. Geographic range is east Kamchatka (USSR) to Yakutat, Alaska (USA). Maximum depth of capture in the Gulf of Alaska is 196 fath (358 m). Absolute abundance appears to be low, and centered in shallow water with juvenile Pacific ocean perch (*Sebastes alutus*). Von Bertalanffy growth constants, for combined sexes, are: $K = 0.18$, and $L_\infty = 31.4$ cm. All females larger (older) than 21 cm (7 years) were mature, and all smaller (younger) than 18 cm (5 years) were immature.

WESTRHEIM, S. J., AND H. TSUYUKI. 1971. Taxonomy, distribution, and biology of the northern rockfish, *Sebastes polyspinis*. J. Fish. Res. Bd. Canada 28: 1621–1627.

Les auteurs récapitulent nos connaissances sur la taxonomie, la répartition, l'abondance et la biologie de la rascasse du Nord, *Sebastes polyspinis* (Taranetz and Moiseev 1933). Ils décrivent les caractères morphologiques et biochimiques du taxon. *Sebastes polyspinis* se trouve depuis le Kamchatka oriental (URSS) jusqu'à Yakutat, Alaska (EU). Dans le golfe d'Alaska, il est capturé à une profondeur maximale de 196 brasses (358 m). L'abondance absolue semble faible et est centrée sur les hauts-fonds avec celle des jeunes perches de mer (*Sebastes alutus*). Les constantes de croissance de von Bertalanffy, chez les sexes combinés, sont: $K = 0.18$, $L_\infty = 31.4$ cm. Toutes les femelles de plus de 21 cm (7 ans) ont atteint la maturité sexuelle alors qu'aucune de moins de 18 cm (5 ans) n'a atteint ce stade.

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IN 1962, the Fisheries Research Board began an investigation of the groundfish resources of the northeast Pacific Ocean that occupy the outer continental shelf and upper continental slope. Primary emphasis was placed on Pacific ocean perch (*Sebastes alutus*), but incidental information was collected on other species. Among these was the northern rockfish (*Sebastes polyspinis*), one of the lesser known scorpaenids in this region.

The purpose of this report is to summarize the available information concerning the taxonomy, distribution, abundance, and biology of *S. polyspinis*.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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Materials and Methods

Most of the *S. polyspinis* specimens for this study were collected during 1963–65, from trawl catches of the C.G.S. *G. B. Reed* (Westrheim 1970). In May 1970, four specimens were collected from *G. B. Reed* catches for electrophoresis analysis (Harling et al. MS 1970). These electrophoresis analyses of hemoglobin were conducted within 2 hr after capture as per Tsuyuki et al. (1968), except that 0.01% each of potassium ferricyanide and potassium cyanide were added to the starch gel to convert all hemoglobins to the cyanmet form. The conversion of oxy- to cyanmet hemoglobin does not measurably alter the electrophoretic mobility, but eliminates the oxidative formation of methemoglobins, which possess a greater cathodal mobility (Tsuyuki and Ronald 1971).

Morphometric and meristic data were collected during 1963–65 from 56 specimens, and other morphological data from 20 of these specimens, and are reported in the format of Phillips (1957) in Appendix Tables 1 and

2. All specimens were collected in the Gulf of Alaska, from Yakutat (ca. 141°W) to Chirikof Island (ca. 156°W). Size range of the 56 specimens was 143–283 mm, standard length, with no more than four males or females per centimeter interval.

Specimens for biological studies were collected from two *G. B. Reed* hauls — GBR 64–8–15 and GBR 65–2–21. Haul no. 64–8–15 was completed on August 5, 1964, off the Shumagin Islands in 58 fath (106 m). All *S. polyspinis* in the catch were measured to the nearest lower centimeter fork length, and a stratified sample (10 fish per cm interval) was taken for detailed examination — sex, maturity, and age (otoliths). Haul no. 65–2–15 was completed on February 20, 1965, off Kodiak Island in 110–114 fath (201–209 m), and approximately 30% of the *S. polyspinis* in the catch were sampled for length and sex.

Maturity was ascertainable only for females. Ovaries containing yellow eggs were deemed mature, and those that were small and translucent were deemed immature. Otoliths were read under reflected light at 10 magnifications with a binocular microscope. The wide, opaque, white bands were considered to represent summer growth zones, and the narrow, translucent, blue zones, the winter "nongrowth" zones.

Description

Sebastes polyspinis (Fig. 1) resembles *S. alutus* in color and body shape, but is unique among *Sebastes* in the Pacific Ocean, east of the Aleutian Islands, in possessing 14 dorsal fin spines — all other *Sebastes* in this region normally have 13. Head spines are weakly developed, and the supraocular, tympanic, coronal, and nuchal spines are absent. For *S. alutus*, the supraocular and tympanic spines are present, particularly among specimens within the size range of *S. polyspinis*. Despite these differences, some difficulty was encountered in sorting *S. polyspinis* from juvenile *S. alutus* in the *G. B. Reed* catches. This similarity may explain in part the absence of *S. polyspinis* in the Gulf of Alaska trawl catch records of Alverson et al. (1964).

Muscle myogen electropherograms of *S. polyspinis* resemble those of *S. ciliatus*, *S. jordani*, and *S. mystinus* (Tsuyuki et al. 1968). Hemoglobin electropherograms of *S. polyspinis* (Fig. 2) are unique for this species, and differ from those of all other rockfish species examined (Tsuyuki et al. 1968). In particular, we wish to point out the differences between the patterns of *S. polyspinis* and *S. ciliatus*, since a previous study (Tsuyuki et al. 1965) indicated that these two species had near-identical hemoglobin electropherograms. Tsuyuki et al. (1968) noted that the discrepancy probably resulted from oxidative changes that occurred in the hemoglobins during the 2 days required to transport the blood samples prior to analysis. It is also apparent that, although the hemoglobins of only four specimens of *S. polyspinis* examined in 1970, one pattern (specimen no. 2) is polymorphic. We do not know whether the variant pattern resulted from a genetically linked polymorph, or from a reproductively isolated sibling species. However, oxidative changes do not explain the difference. A comparison of the four-zone pattern of *S. polyspinis* and the two-zone pattern of *S. ciliatus* indicates how samples from the latter species could easily acquire a four-zone pattern, since oxidative changes can be expected to form additional similarly spaced zones of greater cathodal mobility.

Distribution

Sebastes polyspinis was originally described by Taranetz and Moiseev (Taranetz 1933) from a specimen collected near the Pribilof Islands, Bering Sea. Its range was reported as east coast of Kamchatka to the Pribilof Islands. Schultz (1943) extended the recorded range south and east to the Shumagin Islands. His report contained a translation of the original description, and a key to "North Pacific species of *Sebastodes* with XIV dorsal spines that have a flattish to convex interorbital space." Barsukov (1964) included this species in his key for trawl-caught rockfishes in the Bering Sea and Gulf of Alaska, and reported specimens collected from east Kamchatka (W Bering Sea) to Portlock Bank (Gulf of Alaska). Hitz (1965) included *S. polyspinis* in his field key and noted the range as "Bering Sea and Gulf of Alaska."

During 1963–67, *G. B. Reed* trawling operations in the Gulf of Alaska extended from Dixon Entrance (ca. 54°N, 134°W) to Unalaska Island (ca. 53°30′N, 168°W) (Westrheim 1970; Westrheim et al. MS 1968; and Harling et al. MS 1970). *Sebastes polyspinis* was present in 35 (39.8%) of the 88 hauls completed west of Cape Spencer, Alaska, over a depth range of 40–239 fath (73–437 m). No specimens were caught south of Cape Spencer. Incidence among hauls decreased from Unalaska Island eastward, and from shallow water to deep water. The easternmost documented[1] catch of *S. polyspinis* was one specimen taken in haul 63-6-46 off Icy Bay (59°39′N, 142°27′W) in 98–103 fath (179–188 m) on July 25, 1963. This specimen (male, 211 mm standard length) was deposited in the museum of the Institute of Animal Resource Ecology, University of British Columbia (cat. no. BC64-472). Prior records of *S. polyspinis* in the Institute collection did not include any specimens taken east of 148°W (Pt. Elrington). The *G. B. Reed* collection thus extends the recorded range eastward some 180 miles from Portlock Bank.

Schultz (1943) and Hitz (1965) report the maximum depth of capture as 120 fath (220 m). For the *G. B. Reed* catches, the maximum depth in summer was 140 fath (256 m), and in winter, 196 fath (358

[1]One specimen was collected off Yakutat (59°19.8′N, 141°04′W) in 90–110 fath (165–201 m) on July 18, 1963, but it was not deposited in a museum.

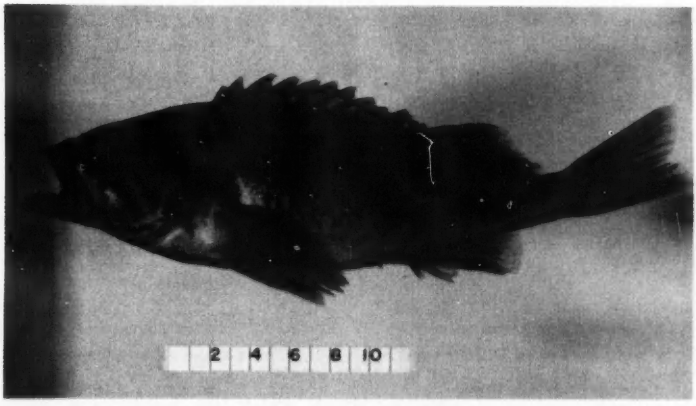

FIG. 1. *Sebastes polyspinis*, scale in centimeters. (Photograph by F. T. Pletcher)

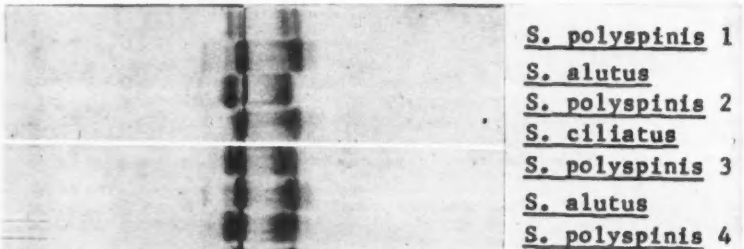

FIG. 2. Hemoglobin electropherograms of four specimens of *Sebastes polyspinis* compared with *S. alutus* and *S. ciliatus*, collected from GBR 70-1-71 off Icy Bay, Alaska, May 1970.

m) — both observations were made off Albatross Bank on the south coast of Kodiak Island.

Abundance

Sebastes polyspinis appears to be a minor component of the rockfish community in the Gulf of Alaska — at least in the depths occupied by adult ocean perch. Catch rates were usually low, and none exceeded 50 lb/hr east of Kodiak Island. In the Kodiak–Unalaska region, relatively high catch rates (103–4935 lb/hr) occurred in conjunction with catches of juvenile ocean perch (mean length, 19–26 cm fork length) at 52–96 fath (95–176 m) in summer and 68–114 fath (124–190 m) in winter.

Andriashev (1937) reported *S. polyspinis* to be common in the Bering Sea. During the USSR 1932–33 trawling explorations, catch rates near the Pribilof Islands were as high as "2 tons per hour (with *S. alutus*)."

Biology

Size Composition

Size ranges (sexes combined) for *S. polyspinis* were 15–30 cm ($\bar{L}$ = 20.9 cm) and 19–37 cm ($\bar{L}$ = 24.1 cm), respectively, for haul no. 64-8-15 and 65-2-21. Both distributions were bimodal (Fig. 3). Corresponding size ranges for *S. alutus* (virtually all juveniles) were 12–26 cm ($\bar{L}$ = 21.1 cm) and 15–32 cm ($\bar{L}$ = 23.1 cm), respectively, for the same two hauls.

Within each haul, *S. polyspinis* size compositions of males and females were similar. Sex ratio was approximately 1:1 — 48.9% males for 65-8-15, and 45.1% males for 65-2-21.

Age Determination

A total of 127 otoliths was collected and each was read independently by two readers without reference to length or sex of the fish. Consistency of readings (percent identical readings) among the readers varied inversely with number of "annuli," but rarely was less than 67% (Table 1). Otoliths from males and females were equally readable.

Table 1. Consistency of readings for 126 otoliths from the northern rockfish, by sex.

	Males		Females	
No. rings	T[a]	%A[b]	T	%A
4	2	100	4	100
5	16	94	11	82
6	15	87	16	81
7	7	71	8	50
8	5	80	4	100
9	6	50	4	75
10	4	75	3	100
11	7	57	6	83
12	1	100	3	67
13	1	0	0	–
14	0	–	2	0
15	0	–	1	100
total	64		62[c]	

[a]T = total otoliths read.
[b]%A = % agreement readings.
[c]One otolith unreadable (crystallized).

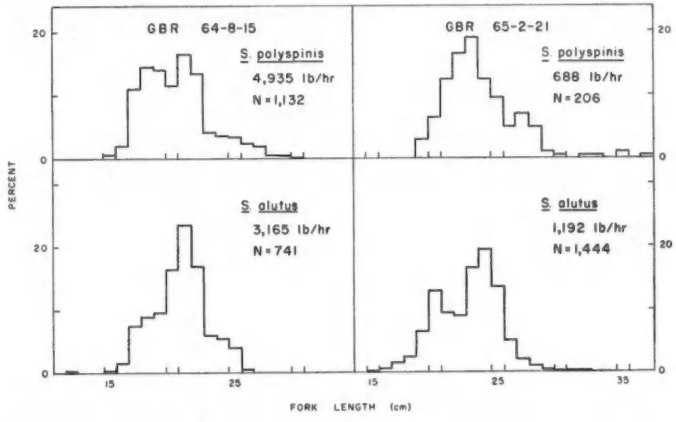

Fig. 3. Size composition, sexes combined, of *Sebastes polyspinis* and *S. alutus* from hauls no. 64-8-15 and 65-2-21.

Age Composition

Assuming that these "annuli" are valid, the age range of the sample was 4–13 years for males and 4–15 for females (Table 2). Age compositions were multimodal for males (modes at 6 and 11 years) and females (modes at 6, 11, and 14 years). These data suggest that survival rates vary appreciably among year-classes, as was noted earlier for *S. alutus* (Westrheim 1970) in this region.

Growth

Since age-group mean lengths were similar for males and females, the combined data for both sexes were used to estimate the Von Bertalanffy growth constants K and L_∞ (Beverton 1954). The results were: K = 0.18 and L_∞ = 31.4 cm. Similar values were reported by Phillips (1964) for two small rockfish species off California — *S. jordani* (K = 0.25, L_∞ = 31.5 cm total length) and *S. saxicola* (K = 0.15, L_∞ = 32.7 cm total length).

Maturity

Examination of the 63 females in the August 1964, stratified subsample indicated that all specimens larger than 21.9 cm were mature and all smaller than 18.0 were immature (Table 3). All

Table 2. Age–length relation for male and female northern rockfish.

Fork length (*cm*)	Age												Total
	4	5	6	7	8	9	10	11	12	13	14	15	
						Males							
16	4	10	–	–	–	–	–	–	–	–	–	–	14
17	–	38	12	–	–	–	–	–	–	–	–	–	50
18	–	33	49	–	–	–	–	–	–	–	–	–	82
19	–	78	16	–	–	–	–	–	–	–	–	–	94
20	–	15	29	–	15	–	–	–	–	–	–	–	59
21	–	–	56	37	0	–	–	–	–	–	–	–	93
22	–	–	46	15	0	–	–	–	–	–	–	–	61
23	–	–	5	5	14	–	–	–	–	–	–	–	24
24	–	–	4	13	4	13	–	–	–	–	–	–	34
25	–	–	–	–	–	4	–	12	–	–	–	–	16
26	–	–	–	–	–	6	6	6	–	–	–	–	18
27	–	–	–	–	–	–	2	2	2	–	–	–	6
28	–	–	–	–	–	–	0	2	–	–	–	–	2
29	–	–	–	–	–	–	1	–	–	1	–	–	2
Total	4	174	217	70	33	23	9	22	2	1	0	0	555
$\bar{L}$	16.5	18.8	20.6	22.4	22.3	25.2	23.9	26.2	27.5	29.5	–	–	
						Females							
15	5	–	–	–	–	–	–	–	–	–	–	–	5
16	2	4	–	–	–	–	–	–	–	–	–	–	6
17	30	45	–	–	–	–	–	–	–	–	–	–	75
18	–	66	17	–	–	–	–	–	–	–	–	–	83
19	–	16	46	–	–	–	–	–	–	–	–	–	62
20	–	15	58	–	–	–	–	–	–	–	–	–	73
21	–	–	56	37	–	–	–	–	–	–	–	–	93
22	–	–	46	46	–	–	–	–	–	–	–	–	92
23	–	–	10	5	10	–	–	–	–	–	–	–	25
24	–	–	–	8	0	–	–	–	–	–	–	–	8
25	–	–	–	–	4	–	8	8	–	–	4	–	24
26	–	–	–	–	0	6	3	0	3	–	0	–	12
27	–	–	–	–	2	4	–	4	4	–	2	–	16
28	–	–	–	–	–	–	–	3	–	–	–	–	3
29	–	–	–	–	–	–	–	1	–	–	–	1	2
Total	37	146	233	96	16	10	11	16	7	0	6	1	579
$\bar{L}$	17.2	18.5	20.9	22.3	24.5	26.9	25.8	26.8	27.1	–	26.2	29.5	

TABLE 3. Maturity of female northern rockfish, by length and age.

Fork length (*cm*)	No. females	% mature	Age	No. females	% mature
15	1	0	4	4	0
16	3	0	5	11	9
17	6	0	6	16	69
18	5	20	7	8	88
19	4	25	8	4	100
20	5	40	9	4	100
21	5	80	10	3	100
22	6	100	11	6	100
23	5	100	12	3	100
24	2	100	13	0	100
25	6	100	14	2	100
26	4	100	15	1	100
27	8	100			
28	1	100			
29	2	100			
Total	63		Total	62[a]	

[a]One otolith unreadable (crystallized).

fish older than 7 years were deemed mature, and all fish younger than 5 years were deemed immature.

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Messrs D. Davenport and W. R. Harling read all the otoliths, collected and compiled most of the morphometric and meristic data, and provided other excellent technical assistance at sea and in the laboratory. Mr S. N. Williscroft carried out the 1970 electrophoretic analysis aboard the vessel.

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APPENDIX TABLE 1. Morphometric ratios and meristic counts for 56 specimens of *Sebastes polyspinis*.

Measurement	Frequency of measurement into: standard length	Frequency of measurement into: head length	Frequency of orbit width into measurement
Length of head	2.9–3.4	–	3.1–3.9
Depth of body at origin of ventral fins	3.0–3.5	0.9–1.2	2.9–3.8
Depth of body at origin of anal fin	3.6–4.4	1.1–1.4	2.4–3.1
Length of base of anal fin	5.7–7.7	1.8–2.5	1.3–2.0
Length of snout	10.6–15.7	3.6–5.0	0.6–1.1
Width of orbit	9.7–11.8	3.1–3.9	–
Width of interorbital space	12.3–15.0	3.9–5.1	0.6–0.9
Width of suborbital bone	–	–	0.1–0.2
Length of upper jaw	6.2–7.4	2.0–2.5	1.4–1.8
Amount that upper jaw projects	–	8.8–20.7	0.2–0.4
Thickness of body	5.6–7.3	1.8–2.5	1.3–1.9
Width of base of pectoral fin	10.3–12.4	3.2–4.1	0.8–1.1
Longest pectoral fin ray	3.5–4.5	1.1–1.5	2.6–3.1
Longest ventral fin ray	4.7–5.7	1.5–1.9	1.8–2.2
Length of ventral fin spine	6.8–9.1	2.2–3.0	1.1–1.6
Length of first anal fin spine	15.0–25.2	4.9–8.0	0.4–0.7
Length of second anal fin spine	7.8–11.6	2.5–3.7	0.9–1.4
Length of third anal fin spine	7.8–10.4	2.5–3.3	1.0–1.4
Longest anal fin ray	5.5–6.9	1.7–2.3	1.5–1.9
Longest dorsal fin spine	7.6–9.9	2.4–3.2	1.0–1.4
Longest dorsal fin ray	6.1–8.0	2.0–2.5	1.4–1.8
Least depth of caudal peduncle	10.0–12.4	3.1–4.1	0.8–1.1
Ventral length of caudal peduncle	4.1–5.0	1.3–1.6	2.1–2.8
Dorsal length of caudal peduncle	5.6–7.2	1.8–2.3	1.4–1.9
Posterior of anus to origin of anal fin	15.9–28.8	5.1–9.4	0.4–0.6
Longest raker on first gill arch	16.1–23.1	4.7–7.0	0.5–0.7
No. of spines and rays in dorsal fin	XIV, 13–16		
No. of spines and rays in anal fin	IV, 7–9		
No. of rays in each pectoral fin	17–19		
Unbranched rays in each pectoral fin	8–11		
No. of rakers on first gill arch	34–38		
No. of pores in lateral line	40–50		
Diagonal rows of scales below lateral line	46–53		
No. of specimens examined	56		
Size of specimens examined	141–283 mm, SL		

APPENDIX TABLE 2. Other morphological characteristics, based on 20 specimens of *Sebastes polyspinis*.

Sebastes polyspinis (Taranetz and Moiseev 1933) northern rockfish.
Range — East Kamchata (USSR) to Yakutat, Alaska.
Greatest depth taken and maximum size — 196 fath; 370 mm, FL (15 inches).
Body color — Reddish under dark grey mottling; flecks of orange on body. Three olivaceous bands radiating posteriorly from eye. Dorsal fins edged in black, olivaceous red on membranes. Caudal fin rays reddish, membranes olivaceous. Pectorals olivaceous above, reddish orange below. Ventral and anal fins reddish orange, edged in red. Maxillary olivaceous, edged in red. Mandible olivaceous. Ventral portion of head orange-red. Belly white.
Mouth and gill cavities — White, with olivaceous speckling.
Peritoneum — Black, or silver with black dots.
Top of head at midorbits — Convex.
Spines on top of head[a] — Weak nasal; occasional parietal, weak; rarely preocular and postocular, both weak. *Supraocular, tympanic, coronal, and nuchal spines absent.*
Parietal ridges — Weak.
The five preopercular spines — First two directed backward, second usually larger. Fifth usually bifid.
The two opercular spines — Moderately strong and sharp.
Supracleithral and cleithral spines — Moderately strong and sharp.
Lower margin of suborbital bone — One blunt spine.
Posterior edge of gill cover — Multifid spine present.
Symphyseal knob — Forward projecting knob.
Raised patch of teeth on tip of jaw — Moderately raised patch present.
End of maxillary — Below rear of pupil.
Maxillaries — Covered with scales.
Mandibles — Covered with scales.
Branchiostegals — Covered with scales.
Ends of pectoral and ventral fins — Tips of pectorals extend beyond tips of ventrals, reaching anus.
Second anal fin spine — Thicker than third. Second does not reach third by one-fifth orbit width (spines depressed).
Spinous dorsal fin membranes — Moderately incised.
Posterior profile of caudal fin — Moderately indented.
Terminal profile of anal fin — Vertical, or with slight posterior slant.

[a]Taranetz (1933) noted the nasal spine buried beneath the skin, but based this description on a large (305 mm, standard length) specimen from the Bering Sea. Hitz (1965) reported all spines on top of head absent. None of the 56 specimens examined by the author and his colleagues lacked the nasal spines, but none were larger than 283 mm, standard length. The absence of the nasal spines may well be a characteristic of the larger specimens.

An Aberrant Strain of the Bacterial Fish Pathogen *Aeromonas salmonicida* Isolated from a Marine Host, the Sablefish (*Anoplopoma fimbria*), and from Two Species of Cultured Pacific Salmon

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EVELYN, T. P. T. 1971. An aberrant strain of the bacterial fish pathogen *Aeromonas salmonicida* isolated from a marine host, the sablefish (*Anoplopoma fimbria*), and from two species of cultured Pacific salmon. J. Fish. Res. Bd. Canada 28: 1629–1634.

Biochemically unique strains of the causative bacterium (*Aeromonas salmonicida*) of furunculosis in fish are described. The strains were first isolated from a marine host, the sablefish, *Anoplopoma fimbria*, and later, from sockeye (*Oncorhynchus nerka*) and chum (*Oncorhynchus keta*) salmon. The strains were essentially identical, and although always isolated from diseased fish cultured in sea or brackish water, they behaved like typical freshwater bacteria.

The outbreaks of furunculosis in local fish-culture facilities were rare events that are thought to have resulted from import of the pathogen in wild carrier fish. In the case of the sablefish that was captured at sea shortly before its death, the infection appears to represent the first instance of spontaneous furunculosis in a marine fish.

EVELYN, T. P. T. 1971. An aberrant strain of the bacterial fish pathogen *Aeromonas salmonicida* isolated from a marine host, the sablefish (*Anoplopoma fimbria*), and from two species of cultured Pacific salmon. J. Fish. Res. Bd. Canada 28: 1629–1634.

L'auteur décrit les souches à caractéristiques biochimiques uniques de la bactérie (*Aeromonas salmonicida*) responsable de la furonculose des poissons. Ces souches ont d'abord été isolées d'un hôte marin, la morue charbonnière *Anoplopoma fimbria*, puis du saumon sockeye (*Oncorhynchus nerka*), enfin du saumon chum (*Oncorhynchus keta*). Les souches sont essentiellement identiques et, bien qu'isolées de poissons malades élevés en eau salée ou saumâtre, se comportent comme des bactéries d'eau douce.

Les éruptions de la furonculose dans notre établissement de pisciculture étaient phénomènes rares qu'on a attribués aux poissons porteurs, à l'état sauvage, de la bactérie pathogène. Pour ce qui est de la morue charbonnière capturée en mer peu de temps avant sa mort, l'infection représente vraisemblablement le premier cas de furonculose spontanée d'un poisson marin.

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STRAINS of the bacterium responsible for furunculosis in fish (*Aeromonas salmonicida*) constitute, with a few possible exceptions (Smith 1963; Ojala 1966; Kimura 1969a, b), a remarkably homogeneous species (Griffin et al. 1952; Eddy 1960, 1962; Ewing et al. 1961; Schubert 1961; Smith 1963; Eddy and Carpenter 1964; Popoff 1969), and traditionally, the organism has been regarded as a freshwater fish pathogen (McCraw 1952). To the author's knowledge, a natural infection with this organism has never been diagnosed in a strictly marine fish. Experimental transmission in sea water has been demonstrated (Scott 1968), and infections acquired in sea water might account for furunculosis in anadromous species such as salmonids. However, the view is widely held that such fish either become infected on reentering fresh water to spawn, or that the pathogen, carried to sea in juvenile salmon, causes the disease in carrier fish when they are later exposed to the stresses of the upstream spawning migration.

The purpose of this report is to describe an aberrant strain of *A. salmonicida* that was initially isolated from a marine host, the sablefish (*Anoplopoma fimbria*), but that has since been isolated from two species of cultured Pacific salmon.

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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Materials and Methods

Bacterial Strains

Seven strains of *A. salmonicida* were studied (strains AS1–AS7). One of these (AS1) was obtained as a reference culture. It was kindly supplied by Dr R. R. Rucker, Western Fish Disease Laboratory, Seattle, Washington, and was isolated on June 9, 1963, from a steelhead trout (*Salmo gairdneri*) at Eagle Creek National Fish Hatchery, Oregon. All other strains were isolated in this laboratory by culturing infected kidney material on plates of TYE agar (Evelyn 1971) or Bacto[1] tryptic soy (TS) agar at 15 or 22 C. Judging from the resulting growth, pure cultures of *A. salmonidica* were always obtained.

Strains AS2 and AS3 were isolated on January 10, 1967, from a freshly dead sablefish (Herman 1968 lists this isolation). This fish had been trawl-caught on December 1, 1966, in Plumper Sound, B.C. Along with other sablefish in the catch, it was being held at this station for growth studies in running sea water at 7 C and 28‰ salinity, and was being fed a diet of frozen herring. Unlike the other sablefish that recovered from minor injuries sustained during capture and transport, this fish developed an increasingly ragged, haemorrhagic superficial lesion ventrally on the caudal peduncle. It fed poorly, or not at all, and at death was markedly anaemic.

Strains AS4 and AS5 were isolated on May 28, 1969, and February 2, 1971, respectively, from frozen rainbow trout (*S. gairdneri*) sent to this laboratory for examination. The trout had been cultured in fresh water in provincial facilities at Abbotsford, B.C. (AS4) and Summerland, B.C. (AS5), and at the time of examination, trout at these facilities were undergoing furunculosis epizootics.

Strains AS6 and AS7 were isolated on June 10, 1970, from a freshly dead, juvenile sockeye (*Oncorhynchus nerka*) salmon, and on July 20, 1970, from a moribund chum (*Oncorhynchus keta*) salmon fingerling, respectively. At the time of the disease outbreaks both lots of fish were being held at this station; the sockeye in diluted sea water at 9‰ salinity and 14.5 C, the chum in sea water at 13 C.

Characterization Tests

These were performed as described elsewhere (Evelyn 1971), but instead of using 3.0% NaCl in the various media, "normal" levels of NaCl (up to 0.5%) were employed.

Amino Acid Requirements

The effect on growth of omitting one or more amino acids was studied at *p*H 6.9 in a basal medium containing the following ingredients per liter: glucose 2.0 g; $(NH_4)_2SO_4$ 1.0 g; NaCl 1.0 g; K_2HPO_4 2.5 g; KH_2PO_4 1.0 g; ferric ammonium citrate 50.0 mg; $CaCl_2 \cdot 2H_2O$ 0.5 mg; $ZnSO_4 \cdot 7H_2O$ 0.1 mg; $CuSO_4 \cdot 5H_2O$ 0.1 mg; $MgSO_4 \cdot 7H_2O$ 10.0 mg. Except for hydroxyproline, which was not used, and cysteine, which does not occur in casein, but which was used at an arbitrary level of 150.0 mg cysteine·HCl per liter of medium, the final concentration of each of the other 18 amino acids tested corresponded to the concentration that would have resulted if the medium had instead been prepared with 0.5% casein (see Dunn and Rockland 1951 p. 218). The amino acid media were sterilized by autoclaving at 121 C for 2–3 min.

Viable Cells

In survival studies, counts of viable cells were determined by serial dilution in TYE broth (see Evelyn 1971).

Results and Discussion

The isolation of the freshwater fish pathogen, *A. salmonicida*, from the sablefish was surprising for two reasons. First, the marine history of the sablefish, both in the wild and in culture, might more logically have led one to expect the involvement of a marine pathogen. Second, a natural infection with *A. salmonicida* had apparently never been recorded in fish cultured in local facilities, and indeed, the only other such infection at this station occurred some 3½ years later when sockeye and chum salmon were affected.

Although it is only possible to speculate, it is believed that the pathogen was imported to this station in carrier fish. In the more recent instance involving Pacific salmon, the pathogen is thought to have been brought in with the sockeye salmon. These were wild fish that had been trapped at Cultus Lake, B.C., approximately 1½ months before they showed evidence of the disease. With the sablefish, the diseased specimen may have represented a carrier fish that was rendered susceptible to the carried pathogen by the trauma of capture and transport. At sea, it might well have contracted the bacterium by eating an infected, migrating juvenile salmon, or by contact with free-floating *A. salmonicida* washed into the sea from a terrestrial source. Under laboratory conditions, strains of *A. salmonicida* survived decidedly better in sea water than in fresh water (Table 1). Further, when 0.1% peptone was added to sea water as a "pollutant," survival was very protracted (at least 80 days). This information indicates that infection by free-floating *A. salmonicida* in sea water is a distinct possibility.

The strains of *A. salmonicida* isolated from the sablefish (AS2, AS3) and Pacific salmon (AS6, AS7) formed a group that was biochemically

[1]Prefix denotes medium was a product of Difco Laboratories Inc., Detroit, Michigan.

TABLE 1. Survival of reference (AS1) and sablefish (AS2) strains of *Aeromonas salmonicida* in various suspending media[a] at 15 C.

Suspending medium	Bacterial strain	Viable cells/0.45-ml sample at time (*days*)							
		0	1	2	3	5	7	12	15
Distilled water[b]	AS1	10^5	0	0	–	–	–	–	–
	AS2	10^6	0	0	–	–	–	–	–
Tap water[c]	AS1	10^6	0	0	–	–	–	–	–
	AS2	10^6	10^3	<10	0	0	–	–	–
1% NaCl	AS1	10^7	10^3	10^2	0	0	–	–	–
	AS2	10^6	10^3	0	0	–	–	–	–
3% NaCl	AS1	10^5	0	0	–	–	–	–	–
	AS2	10^6	0	0	–	–	–	–	–
75% sea water	AS1	10^5	10^7	10^6	10^5	10^4	0	0	–
	AS2	10^6	10^5	10^4	10^4	10^3	<10	0	0
Sea water[d]	AS1	10^6	10^6	10^5	10^5	10^4	10^3	<10	0
	AS2	10^6	10^4	10^3	10^3	10^3	<10	0	0

[a]Suspending media were sterilized by autoclaving (121 C, 10 min) and were incubated static between samplings.

[b]Triple glass-distilled water.

[c]Tap water was of a quality used in the routine culture of salmonids.

[d]Sea water (3.1% salt when dried to constant weight at 110 C) was taken from Departure Bay, B.C., and clarified by filtration (0.45-μ pore diameter Millipore filter).

distinct from the strains isolated from the steelhead (AS1) and rainbow (AS4, AS5) trout. The last three strains were regarded as reference strains, since, except for one or two features indicated in Table 2, they were archtypical of *A. salmonicida*.

The strains were all very similar in cell morphology, growth characteristics, and in the conditions of temperature (20–25 C), *p*H (6.0–7.0), and salinity (0.75–1.0% NaCl) required for fastest growth. Since most of these features have already been described in detail by other authors (see especially Griffin et al. 1952), only the barest details are reiterated here. Morphologically, young (48-hr) cells from TYE or TS agar were predominantly cocci or short, round-ended, gram-negative, nonacid-fast, aflagellate, nonmotile rods. Spores and capsules were never produced. On each of these media, 24- to 48-hr colonies were typically punctiform, and the red-brown, water-soluble, diffusing pigment, characteristic of the species, was usually clearly evident by 72–96 hr. Growth developed slowly at 1–3 C, but at 37 C, *p*H 5.0 or with 5% NaCl, no growth occurred and the strains were slowly killed.

Interestingly, after 2 years of subculture on TYE agar, one of the sablefish strains (AS3) lost its ability to produce the red-brown diffusing pigment, but otherwise remained unchanged. Pigment production may therefore be a somewhat less stable feature of *A. salmonicida* than has hitherto been thought. Strains incapable of producing pigment are known to occur naturally (Smith 1963; Kimura 1969a) and it is possible that they are more frequently overlooked than is generally realized.

The biochemical properties of the reference strains are presented in Table 2. The sablefish and Pacific salmon strains differed from these as follows. They produced (strong) indole and acetoin reactions, oxidized gluconate, produced acid and gas from sucrose and cellobiose, but failed to hydrolyze Tween 80, or to ferment sorbitol, salicin (strain AS2 showed a weak, delayed reaction), and mannitol (strains AS2 and AS6 produced acid and gas at 10–14 days). They also produced much stronger catalase and lysine decarboxylase reactions than the reference strains, and their gas production from carbohydrates was more delayed, lagging acid production by 2–3 days.

Nutritionally, the growth requirements of the sablefish and Pacific salmon strains were more complex than those of the reference strains. Perhaps for this reason, they produced, at most, microscopic colonies on Bacto nutrient agar, and grew more poorly in synthetic mixtures of amino acids than with yeast extract in equivalent (0.5%) concentration. In both instances, the opposite was true for the reference strains. The strains from the sablefish and Pacific salmon shared with the reference strains a requirement for arginine and methionine, but differed from the reference strains

TABLE 2. Biochemical characteristics[a] of reference strains (AS1, AS4, and AS5) of *Aeromonas salmonicida*.

Test	Result
Oxidase reaction (Kovacs 1956; Ewing 1962); fermentative and aerogenic with glucose (Hugh and Leifson 1953); catalase produced[b]; β haemolysis on human blood; litmus milk reduced and peptonized; gelatin hydrolyzed; lipolysis with Tween 40[c] and Tween 80[c]; nitrate reduced to nitrite; alkaline reaction with arginine; lysine decarboxylated[b]	Positive
Production of indole, acetoin[d], 2,3-butanediol[d], hydrogen sulphide, urease, ornithine decarboxylase, or phenylalanine deaminase; gluconate oxidation; growth in Koser's mineral solution with citrate, malonate, or glucose	Negative
Reaction with glucose; galactose; fructose; mannose; maltose; trehalose[e]; dextrin; starch; glycogen; glycerol; mannitol; sorbitol[b]; salicine	Acid and gas
Reaction with arabinose; rhamnose; xylose; lactose; sucrose; melibiose; cellobiose; raffinose; melezitose; inulin; adonitol; inositol; dulcitol	No acid or gas
Reaction to the vibriostatic agent (0/129)[f]; penicillin[g]; novobiocin[g]	Resistant
Reaction to terramycin; aureomycin; chloromycetin	Sensitive
Growth without arginine or methionine	Negative
Growth without lysine; histidine; glutamic acid; aspartic acid; glycine; alanine; leucine; isoleucine; valine; serine; threonine; tryptophan; tyrosine; phenylalanine; proline; cystine; cysteine	Positive

[a]Based on descriptions of *A. salmonicida* provided by various authors (Griffin et al. 1952; Eddy 1960, 1962; Ewing et al. 1961; Schubert 1961; Smith 1963; Bain and Shewan 1968; Popoff 1969) the strains are virtually archtypical of *A. salmonicida*. An archtype, however, would ferment arabinose but not sorbitol, and some uncertainty exists as to whether methionine would be essential for growth (see description of *A. salmonicida* in Breed et al. 1957) or merely stimulatory (O'Leary et al. 1956).

[b]Weak reaction.

[c]Polyoxyethylene sorbitan ester of palmitic acid (Tween 40) or oleic acid (Tween 80).

[d]Several media used: Bacto MR-VP medium; TYE broth containing 0.5% glucose; three broth media listed in Cowan and Steel (1965), p. 111.

[e]Delayed reaction.

[f]Compound 0/129 (2,4-diamino-6,7-di-isopropyl pteridine).

[g]Fuzzy zones of inhibition produced, but only with the highest levels of antibiotic tested (penicillin, 10 units; novobiocin, 30 μg).

in their almost absolute requirement for lysine, valine, and isoleucine. Also, in contrast to the reference strains that were virtually unaffected by the combined omission of the aliphatic amino acids glycine, alanine, leucine, isoleucine, and valine, they showed essentially no growth with this treatment.

When the sablefish strains were first isolated, some doubts existed as to their exact identity. These doubts arose because of the novel host involved, and because of the rather unique biochemical features of the strains. However, on the basis of their overall characteristics, and because they were susceptible to *A. salmonicida* bacteriophage and were strongly agglutinated by anti-*A. salmonicida* serum, there can be little doubt that the strains were merely aberrant forms of *A. salmonicida*.

Because detailed biochemical tests are not routinely performed in diagnosing furunculosis, little is known about the incidence of the unusual strains. However, globally it must be low as none of the comparative studies on *A. salmonicida* describes such strains (see Griffin et al. 1952; Eddy 1960, 1962; Ewing et al. 1961; Schubert 1961; Smith 1963; Popoff 1969). In the northwestern United States, however, it is possible that aberrant strains constitute a sizeable proportion of the *A. salmonicida* isolates. This possibility is suggested by extrapolation from the serological findings of Klontz and Anderson (1968). They studied the sablefish strain (AS2) under the designation "file no. 56" and found it to be antigenically indistinguishable from approximately one-quarter of the strains from the hatcheries of the northwestern United States. Taken in conjunction with the present findings it may be that the aberrant strains are indigenous to the Pacific Northwest.

The presence of the aberrant strains in freshwater hatcheries of the Pacific Northwest would not be surprising as, based on their salt requirements for growth, they behaved like freshwater, rather than marine, forms. Thus, despite the fact that they were always isolated from fish in brackish or sea water,

and survived best in suspending media prepared with a seawater base, they did not require salt for growth, and grew best with NaCl levels similar to that optimum for another freshwater bacterium (*Aeromonas liquefaciens*) tested in parallel.

The strains from the sablefish and Pacific salmon were similar in many respects to the aberrant strains of *A. salmonicida* from Japan described by Kimura (1969a, b). The present strains and those of Kimura were highly unusual because they attacked sucrose and cellobiose, and showed evidence of instability in the production of the diffusible, red-brown pigment (present strains), or failed to produce the pigment (Kimura's strains); they were unique in producing indole and acetoin. To date, strains of *A. salmonicida* have not shown a continuum of aberrant features that would tend to link them to the motile members of the genus. Consequently, the relation between *A. salmonicida* and the motile aeromonads has been seriously questioned (Smith 1963). Taxonomically, these strains are therefore very interesting, since in their aberrant features they resemble missing links.

These unusual strains may prove to be a useful and relatively simple means of assessing the effectiveness of measures that are now evolving to prevent the spread of fish disease. The strains possess a combination of unusual features that might be used to trace their spread, and biochemical methods required to recognize the organisms would certainly be more readily accomplished in the average laboratory than methods based on serology (Klontz and Anderson 1968) or bacteriophage (Popoff and Vieu 1970).

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The author thanks Prof L. A. McDermott, Department of Microbiology, University of Guelph, Guelph, Ont., for kindly running the sablefish strain through the diagnostic phage-susceptibility and agglutination reactions, Mr G. Hoskins for his excellent technical assistance throughout this work, and Drs L. Margolis and G. R. Bell for their constructive criticisms during the preparation of the manuscript.

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Note added in proof:

After this paper was accepted for publication, the author learned of the existence of the following thesis: Chudyk R. V. 1965. Numerical taxonomy of *Aeromonas salmonicida*, the causative agent of furunculosis disease in fish (University of Guelph, Guelph, Ont.). The thesis confirmed that strains of *A. salmonicida* (231 of 233 strains from various locations) constituted a homogeneous group of organisms. Further, the organisms were essentially identical to the reference strains used in the present study. (A few apparent differences occurred in the arginine, sorbitol, and catalase reactions, and in gas production from carbohydrates, but these were likely due to differences in methodology and to difficulties in interpreting feebly positive reactions.) Unfortunately, data on some tests, notably the indole and acetoin tests in which certain of the present strains were aberrant, were not given.

An additional outbreak of furunculosis occurred at this station in July–August 1971. Only sablefish (three adjacent lots) were affected. The causative agent was again found to be the aberrant strain of *A. salmonicida*. The sablefish had all been captured in coastal B.C. waters and had been cultured for periods ranging from 2 weeks to 2 years. In the wild, the sablefish may have initially been infected by feeding on raw salmon products since fish in two of these lots were captured in the immediate vicinity of an operating salmon cannery.

Growth Responses of Young Sockeye Salmon (*Oncorhynchus nerka*) to Different Diets and Planes of Nutrition

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BRETT, J. R. 1971. Growth responses of young sockeye salmon (*Oncorhynchus nerka*) to different diets and planes of nutrition. J. Fish. Res. Bd. Canada 28: 1635–1643.

The growth rate and food conversion efficiency of yearling sockeye salmon (*Oncorhynchus nerka*) (26 ± 2 g) was determined for Halver's test diet, Clark's chinook mash, Abernathy pellets, frozen marine zooplankton, and sockeye mash, using a number of planes of nutrition. The maximum growth rates at 15 C varied from 3.1% dry body wt/day (Halver's) to 1.5%/day (marine zooplankton) with corresponding gross conversion efficiencies of 48 and 10%. Maintenance rations were determined, mostly by extrapolation, and used to evaluate the net conversion efficiency for each diet. The highest was 74% net conversion on Halver's test diet. Although major differences in growth response existed between the five diets, it was concluded that the various moist diets based on fish meal, used in these and earlier experiments, were not significantly different from each other when on the same plane of nutrition.

BRETT, J. R. 1971. Growth responses of young sockeye salmon (*Oncorhynchus nerka*) to different diets and planes of nutrition. J. Fish. Res. Bd. Canada 28: 1635–1643.

Nous avons mesuré le taux de croissance et l'efficacité de conversion des aliments chez les saumons sockeye (*Oncorhynchus nerka*) d'un an (26 ± 2 g) soumis aux régimes suivants, appliqués à des paliers de volume différents: diète expérimentale de Halver, purée de saumon chinook de Clark, boulettes d'Abernathy, zooplancton marin congelé et purée de sockeye. Le taux maximal de croissance à 15 C varie de 3.1% du poids sec du corps par jour (diète de Halver) à 1.5% par jour (zooplancton marin) avec efficacité de conversion brute de 48 et 10% respectivement. Nous avons préparé, le plus souvent par extrapolation, des rations de subsistance dont nous nous sommes servi pour évaluer l'efficacité de conversion nette de chaque régime. Le taux de conversion nette le plus élevé a été de 74% avec la diète de Halver. Bien qu'il existe des différences majeures dans les poussées de croissance résultant de ces cinq régimes, nous avons conclu que les purées à base de farines de poisson utilisées dans ces expériences-ci et dans de précédentes ne diffèrent pas appréciablement les unes des autres lorsqu'appliquées sur un même palier.

Received March 22, 1971

OVER the past 7 years, experiments have been conducted on the effect of temperature and ration on growth rate of young sockeye salmon, *Oncorhynchus nerka* (Brett et al. 1969). In addition, growth has been accelerated by favorable manipulation of a set of environmental factors — temperature, salinity, photoperiod, and water velocity (Brett and Sutherland 1970). The composition of the food has varied between experiments, starting with a laboratory-prepared diet (recorded in Brett et al. 1969) and proceeding to a number of commercial products.

Because of this variety of foods, a comparison was made of sockeye growth rates and food conversion efficiencies, using five diets (see Table 1 and Appendix 1) including two based upon natural foods. It was of interest to know how these related when fed at more than one plane of nutrition and to what extent artificial and commercial foods matched or exceeded typical natural[1] foods (fresh frozen zooplankton, fish) so that broader interpretation could be made of existing data. A further aim of the research was to assess the extent of potential differences in growth response that the experimenter faces when selecting one diet, and to

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

[1]Many commercial foods include components that are natural, e.g., fish meal. These, however, do not generally exceed more than one-third of the composition.

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TABLE 1. Percentage composition (determined by proximate analysis) and calculated caloric content (kcal/g) of diets.

Diet	Water	Protein		Fat		Carbohydrate[a]		Ash[b]		Caloric content[c]	
		Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Halver's	67.0	16.5	50.0	3.0	9.0	9.6	29.0	4.0	12.0	1.35	4.10
Clark's	9.5	62.6	69.2	13.0	14.3	8.1	8.9	6.9	7.6	4.17	4.61
Abernathy[d]	32.4	32.5	48.1	9.6	14.2	17.2	25.5	8.3	12.3	3.02	4.47
Marine zooplankton	89.0	6.4	58.2	2.4	21.8	<0.1[e]	<0.3	2.2	20.0	0.49	4.49
Sockeye mash	76.0	16.0	65.0	6.3	25.6	<0.2	<0.5	2.3	9.4	1.24	5.14

[a]In some instances this is equivalent to nitrogen-free extract, determined as: (dry feed) — (protein + fat + ash).
[b]Ash determined by difference.
[c]Caloric content determined as the maximum metabolizable energy (physiological value) assuming full digestibility. Equivalents used (kcal/g): protein = 4.2, fat = 9.4, carbohydrate = 4.0.
[d]Composition supplied by R. E. Burrows, Longview, Washington.
[e]Chitin was not determined. Since it is not digestible, available carbohydrate would be very low.

recognize the limitations of comparison between experiments when diets and planes of nutrition are not standardized.

The choice of marketed "feeds" was purely circumstantial, according to what was readily available in the Pacific Northwest. It must be recognized that the formulations are constituted by different manufacturers to be suitable for any particular one (or all) of the three species of cultured Pacific salmon (*O. nerka*, *O. kisutch*, and *O. tshawytscha*). Nutritional advances are constantly being made. No marketing significance can be attached to the results.

Experiments were conducted in the midsummer period, when ambient temperatures of 14–16 C approximated the best temperatures for growth of young sockeye (Brett et al. 1969).

Materials and Methods

The Fish

Yearling sockeye salmon that had been cultured on Abernathy pellets were sorted for fairly uniform size (14.1±0.6 cm; 25.9±2.2 g SE) and randomly distributed into 10 tanks. Owing to a shortage of some of the diets, only 26 fish were used per tank. During the period of July 24–August 20, the fish (in pairs of tanks) were introduced to the new diets, which were presented in excess for 4 weeks.

Under light anaesthetic (60 ppm M.S. 222), all fish were weighed to the nearest 0.01 g every 2 weeks and returned to the tanks. Surface water was removed by rolling each fish in a moist cloth.

The moisture content of two fish from each tank was determined on August 20, the starting date for controlled rations (or planes of nutrition). The pooled mean content was 77.6±0.8% water (±SE; n = 20). Every 2 weeks thereafter, up to the 6th week, eight fish were removed from each tank for moisture determination. Thus, following the initial pooled determination, one-third of the fish were killed at each weighing. Total body composition (protein and fat) was calculated from the wet weight and body water content, using the equations relating these components, derived for sockeye by Groves (1970).

The Diets

The composition of each of the five diets (Table 1) was determined by proximate analysis (using standard methods — described in Brett et al. 1969; see also Love 1970) and the caloric content calculated. Ingredients of the three formulated diets are included in Appendix 1 (see Fowler and Banks 1969; Halver 1970). Two of the diets (Halver's and sockeye mash) were prepared fresh every 2 weeks. All diets were stored at –10 C. Three days' supply was regularly removed and kept in small insulated jars at 0 C for immediate use in feeding. The particulars regarding experimental preparation and feeding were as follows:

(1) *Halver's test diet* — This was prepared warm and poured into trays to a depth of about 2 cm. When chilled, it was diced by slicing into small cubes (approximately 3 mm³) and weighed in an aluminum dish, and the prescribed amount spooned out at a slow steady rate.

(2) *Clark's chinook mash* — "Swim-up" mash was formed into dry pellets using a California pellet mill (orifice size 3/32 inch, 2.4 mm). The pellets were screened for uniform size and removal of "dust," then weighed to within 0.01 g for rationing.

(3) *Abernathy pellets* — The ⅛-inch size (3.2-mm) moist pellet was taken readily by the yearling fish. Particles reaching the bottom of the tank were allowed to be eaten before presenting the remainder of the ration.

(4) *Marine zooplankton* — Collected in the Strait of Georgia, B.C., in June, zooplankton[2] samples were

[2]Almost entirely mature *Calanus plumchrus*.

frozen in waxed cartons. The top 1 cm was subsequently removed because of relatively high moisture content that collected at the surface. Using a cork borer, 3/32-inch diameter cores were ejected onto an ice-coated tray, cut into small lengths, and stored in insulated jars. To avoid any possible vitamin deficiency from initial handling and storage, a supplement of 0.25 g/kg of food was added (Appendix 1).

(5) *Sockeye mash* — From the original stock of sockeye, small samples were killed, put through a meat grinder, and formed into a smooth mash in a Waring Blendor. A small amount of salt and skim milk was added to form a paste. A garlic press was used to express the food through 3/32-inch holes.

Part way through the experiment it was decided to add 2.7% gelatin to improve the adhesive propreties. It was immediately apparent that the earlier formulation was inferior, since a slight turbidity, arising from fragments of dispersed tissue during feeding, was eliminated. This correlated with an increase in growth rate from 1.23 to 2.01%/day, on an average ration of 8.3%/day. The addition of the small amount of gelatin could only account for $\frac{1}{10}$ of the observed increase in growth rate (assuming a 33% gross conversion efficiency), and hence cannot be considered as providing the improvement solely on nutritional grounds. Consequently, the data for this diet were considered as two separate sets: sockeye mash no. 1 and no. 2 (with gelatin).

The Tanks

The standard tank for all our growth experiments has been an oval, 197-liter (43-gal) Fiberglas tank (Alderdice et al. 1966). Flushing rate was approximately 400 liters/hr, with a recirculated tank velocity of 9–15 cm/sec (0.3–0.5 ft/sec). Ambient temperatures averaged 15.4±0.17 C (SE) and ranged from 16.9 C at the start to 14.0 C at the end. Photoperiod was constant at 13 hr (7:00 AM–8:00 PM). No oxygen depletion below 94% saturation occurred.

The Rations

Since the relative growth rates of fish on different diets could be differentially affected by the level of ration, it was decided to use two levels, a "high" ration (approximately 7% dry body wt/day) and a "medium" ration (approximately 4% dry body wt/day), applied throughout the 6-week period. This selection proved to be suitable where the diet provided sufficient available calories to promote good growth, but unsuitable otherwise. Also, the more nutritious diets induced greater changes in body constituents (higher fat) than had been anticipated, so that in some instances the actual ration was subsequently determined to be decidedly less than the prescribed. It proved to be necessary to increase the "medium" ration in one instance (marine zooplankton) to obtain better growth rates. Consequently the data were analyzed as three 2-week growth increments with accompanying derived rations. This provided six determinations for each diet (except one tank of accidentally lost fish — on zooplankton). An increase in the number of ration *levels* decreased the number of observations associated with the corresponding group of growth rates, and hence increased the variance. Consequently, general comparison between diets was made on the basis of the growth rate vs. ration curves, assuming a linear relation over most of the range (Fig. 2). Direct comparison was made of instances where questionable differences in growth rate between diets arose, using Student's *t*-test (Table 2). The test was applied only where the rations were approximately the same or somewhat less in the case of the "superior" diet, i.e., not biased in favor of the more effective diet.

Results

Growth Rates

Differences in growth response were apparent very early in the experiment. Even during the 4-week diet introduction period, when excess was pre-

TABLE 2. Diet comparisons according to growth rate (% dry body weight/day) using Student's *t*-test (Fisher and Yates 1963). Grouped mean growth rates (G) and corresponding ration level (R) are shown.

Diets			*t*	df	Significance
Halver's–2.8% G (5.8% R)	>	Clark's–2.2% G (6.2% R)	3.34	62	$P<.01$
Halver's–1.0% G (3.5% R)	>	Clark's–0.8% G (3.6% R)	1.14	57	NS
Clark's–2.2% G (6.2% R)	>	Abernathy–1.8% G (7.1% R)	3.09	62	$P<.01$
Clark's–0.8% G (3.6% R)	>	Abernathy–0.5% G (3.7% R)	2.00	59	$P=.05$
Sockeye mash no. 2–2.0% G (8.2% R)	>	Abernathy–1.8% G (7.1% R)	0.23	62	NS

sented, noticeable size differences developed (Fig. 1). These persisted under the fixed ration levels indicating that more than just diet acceptance was involved in the early period. As a result, on the actual starting date of prescribed rations a small but significant size difference was present between the extremes, i.e., 31.8 ± 1.5 g wet weight on Abernathy, the original diet, and 27.0 ± 2.2 g on marine zooplankton. All diets, however, were taken ravenously.

Determining the relation of growth rate to ration (Fig. 2) provides a means of comparing growth responses for similar interpolated ration levels. The lines obtained for the various diets represent major segments of the overall curves that characterize the ration–growth relation (Thompson 1941; Warren and Davis 1967; Brett et al. 1969). The general form is suggested by the extrapolations in Fig. 2 (dotted lines). A common rate of loss of body weight would obviously occur at 0 ration (starvation). The maximum daily ration is indicated at the termination of each line, from observations where the ration for each diet was increased to the point of satiation in a few feedings. The positions are only approximate. The order of growth response (percent gain in dry weight per day) calculated on the basis of a *fixed* ration of 6% dry body wt/day was: Halver's (2.8%) > Clark's (2.0%) > Abernathy (1.2%) ≷ sockeye mash (no. 2 = 1.1; no. 1 = 0.5%) > marine zooplankton (0.1%).

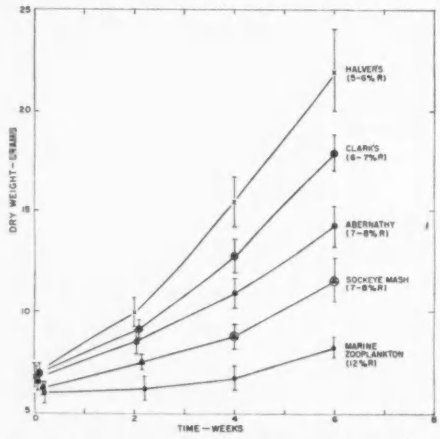

FIG. 1. Growth of yearling sockeye at 15 C when fed on five different diets. Approximate level of ration (R) shown in parentheses as percent dry body weight per day. Sockeye mash was altered in formulation after the 2nd week (circled points). An introductory period of 4 weeks on excess rations was allowed for adapting to new diets. Prescribed planes of nutrition were applied at "zero time." Limits: ±2 SE.

As will be discussed at greater length, comparisons are not strictly valid on a *fixed* ration, since fish may be disposed to consume considerably more of one diet than another. High fat content can depress appetite; diets with large bulk (e.g., water, collagen, chitin) may be consumed in greater daily amounts. Assuming that the *maximum* daily rations are correct estimates, as presented in Fig. 2, the order remains the same but the difference is not as great. The estimates of growth rate (G) and accompanying maximum ration (R) in percent dry body weight per day are: Halver's (G = 3.4% for R = 7.5%) > Clark's (G = 2.9% for R = 8.1%) > Abernathy (G = 2.4% for R = 9.2%) ≷ sockeye mash no. 2 (G = 2.2% for R = 8.6%) > marine zooplankton (G = 1.5% for R = 14.2%).

Yet another comparison can be made, namely, on the basis of the *maintenance* ration (R_m, for G = 0%). Estimates of R_m from Fig. 2 place these as follows: Halver's (2.2%), Clark's (2.5%), Abernathy (2.8%), sockeye mash (3.3–4.2%), marine zooplankton (5.8%).

Conversion Efficiencies

The *gross* efficiency may be determined by calculating G/R × 100%. The curve relating efficiency to ration tends to be domed or hook-shaped, passing through an optimum. These have been determined for each diet (Fig. 3). A high average efficiency of 48% was obtained for Halver's (R = 5.8%/day); that for marine zooplankton was approximately 10% (R = 10–12%/day). As might be expected, the same relative order as that for growth rates was obtained for the various diets.

Since the digestive processing and metabolic costs (SDA or calorigenic effect) could account for much of the difference between diets, calculation of *net* efficiencies ($\frac{G}{R - R_m} \times 100\%$) was made as a further means of examining the relative contributions to growth. The lines of Fig. 4 were determined by selecting a series of points from the derived curves of Fig. 2.

In general, the same order of difference between diets was found to exist for net as for gross efficiency. It is apparent (Fig. 4) that any possible difference between Abernathy and sockeye mash is attributable to the estimate of maintenance ration, which, as stated, was not as well defined as the others because of the switch in diet to include gelatin.

Discussion and Conclusions

Basis of Comparison

Growth experiments have been conducted using a variety of food conversions based on wet weight,

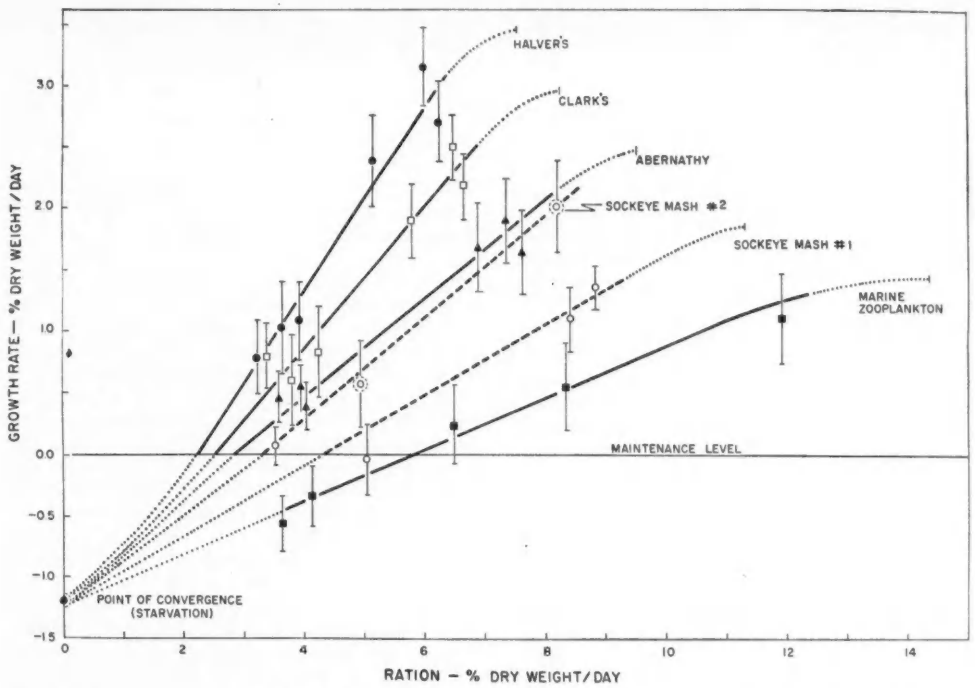

FIG. 2. Growth rate of sockeye in relation to ration for various diets. Limits: ±2 SE. All solid lines determined by least squares. Broken lines for sockeye mash were drawn by eye; two encircled points were for no. 2 formulation. The "point of convergence" was estimated by extrapolation. Dotted extensions of lines indicate expected shapes of curves terminating at maximum voluntary food intake.

dry weight, caloric value, or protein content. The least revealing for most interpretations is that based on wet weight. Dry weight determinations remove the error introduced when food and resulting flesh have different moisture contents, but still retain a lesser error attributable to the difference in energy density (kcal/g) of the dry fractions. The extent of this error in energetic evaluation is indicated in Fig. 5 for two diets and two planes of nutrition. Although the caloric content of the food was static, the caloric content of the dry weight of the fish on Halver's diet increased from 6.12 kcal/g at the start to 6.80 kcal/g by the 6th week (on "high" ration). By contrast, the zooplankton-fed fish, on a "medium" ration, fell to 5.56 kcal/g, a difference of 22% between the extremes in body composition. This would produce a corresponding effect on the diet comparisons.

As Gerking (1971) and others (e.g., Pandian 1967; Tiemeier et al. 1965) have pointed out, the essential aspect of growth is protein elaboration, the basis of cellular increase. In consequence, the efficiency of nitrogen retention is taken as the fundamental element for growth efficiency calculations. This interpretation is not without some limitations, however, since N-retention is influenced by the sparing action of carbohydrate and lipid on the utilization of protein as an energy source (Maynard and Loosli 1962; Phillips 1969). Hence, the best diet formulation must incorporate the best balance of protein (P) and energy (E) sources (P/E ratio).

Since Halver's diet had the lowest energy density (Table 1), it can only be deduced that digestibility, vitamin content, and P/E ratio are favorably balanced, a conclusion that is supported by a high net efficiency.

DIET COMPARISONS

Fowler and Banks (1969) found no difference in the wet-weight growth rates of young chinook salmon (*O. tshawytscha*) when fed equal rations of Abernathy or Oregon pellets (weight increase

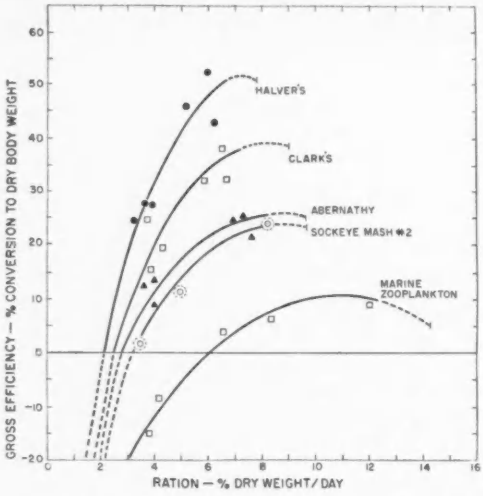

FIG. 3. Gross food conversion efficiencies of various diets. Extrapolations made from curves in Fig. 2.

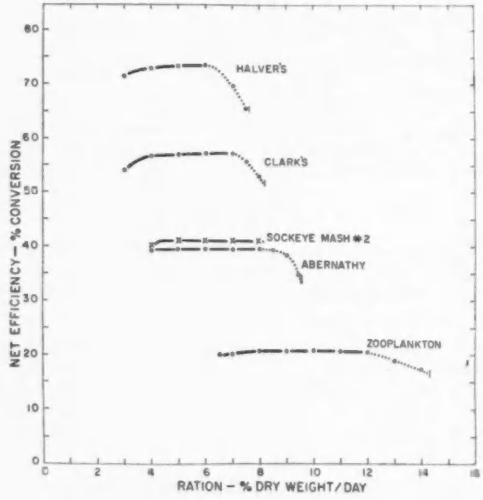

FIG. 4. Net food conversion efficiencies of various diets. Each point was derived by using the appropriate curve and estimate of maintenance ration in Fig. 2.

was from 1.5 to 27 g; average G 1.7%/day; temperature 12 C). Vitamin fortification with C and D proved to be only of slight benefit, if at all.

The fish meal ingredients of Oregon pellets were studied by Westgate et al. (1964) who used Duncan's multiple range test for ranking the fish source. The

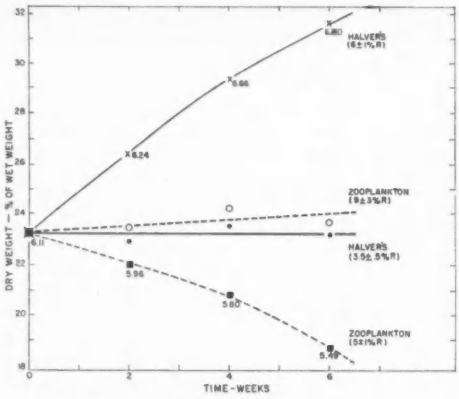

FIG. 5. Change in percentage dry weight of yearling sockeye on two diets at two planes of nutrition. The caloric values (kcal) of a gram of dry body substance are indicated near the points for the upper and lower curves (calculated from proximate composition).

resulting order of diet suitability was dogfish > tuna viscera > salmon viscera > turbot > control; the differences, however, were slight, based mainly on food conversion efficiency and energy density. Statistically significant growth in wet weight was not apparent by parametric analysis (Student's *t*-test, as subsequently checked from data).

Since the Abernathy and sockeye mash no. 2 showed no significant difference, and these are not different from Oregon pellets (which can be equally effectively formulated from various fish species), it is apparent that well-balanced wet pellets, using fish protein, provide comparable growth responses in sockeye fingerlings. Our earlier wet diet, based on canned salmon (Brett et al. 1969), was used to correctly predict the growth rate obtained with Abernathy diet on a restricted ration of 4%/day (in Brett and Sutherland 1970). These tests ran from 14 to 32 weeks. Comparisons between years and between different environmental conditions imposed in our laboratory are therefore not confounded by different wet diets. Dry diets and casein-based diets apparently enhance growth, as formulated.

ZOOPLANKTON DIET

Since marine zooplankton is the very food of young sockeye as they first enter the sea, it is a biologically correct diet. Its comparatively low conversion efficiency as a frozen food was unexpected.

Very few experiments have been conducted where efficiency of conversion of crustacean food

could be determined. Pandian (1967) fed measured rations of fresh fish (*Gambusia affinis*) and prawn (*Metapenaeus monoceros*) to the fish *Megalops cyprinoides*. Gross conversion efficiency was about 10% less on prawn than on fish, mainly from a difference in protein elaboration, possibly because of a basic difference in amino acid balance (see Phillips et al. 1966; Cowey and Corner 1962). The average efficiency was about 25% (40–100-g fish) and rose with decreasing fish weight to about 35% at 10 g.

Using live marine zooplankton, LeBrasseur (1969) related ration (prey concentration) to growth of juvenile chum salmon (*O. keta*) in salt water. Growth was excellent, reaching between 5 and 6%/day at the highest feeding rates. On a wet weight basis, the conversion rate ranged from 33% (R = 16%/day) to 60% (R = 6%/day). Maintenance ration was less than 1%/day. A similar method has been used by R. M. Biette (personal communication) experimenting with ration × temperature effects on underyearling sockeye feeding on natural live zooplankton (mostly *Diaptomus* and *Cyclops*). On a dry weight basis, the conversion efficiency was about 21% at a high ration; maintenance ration was close to 5%/day.

It is apparent that *live* crustacean food can be efficiently converted, although it may be somewhat inferior to fish food. In the frozen state, it is obviously quite inferior. Similar results have been reported using frozen *Daphnia magna* (Anon. 1970). Microscopic examination of the individual zooplankton revealed some ice-punctured cells, together with some free exoskeletons. Rapid freezing might avoid both soluble and insoluble organic loss from fragmented pieces. Until such time as a solution is found, diets formulated from fish meal can be expected to provide considerably better growth.

It can be concluded that experiments that have been conducted in our laboratory using moist diets (Brett et al. 1969; Brett and Sutherland 1970; Brett 1971) display differences in growth rate that are independent of the diet formulation.

Acknowledgments

It is a pleasure to acknowledge the technical assistance of Messrs D. B. Sutherland and G. D. Heritage. Many of the calculations and statistical analyses were performed by Mr Heritage. The marine zooplankton was kindly supplied by Dr R. J. LeBrasseur. Further, in a more indirect way but no less meaningful, the broad interest in biological problems that Dr and Mrs Berkeley always engendered has contributed greatly to the stimulus for conducting experimental work over many years at the Nanaimo Biological Station.

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APPENDIX 1. Ingredients of formulated diets, as supplied by source.

(1) Halver's complete test diet (Western Fish Nutrition Laboratory, Cook, Washington)

Basic composition	%	Vitamin mix		Mineral mix	
Vitamin-free casein	12.7	Thiamin HCl	5 mg	USP XII No. 2	plus
Gelatin	4.0	Riboflavin	20	AlCl	15 mg
Corn oil	3.0	Pyridoxine HCl	5	$ZnSO_3$	300
White dextrin	9.3	Choline chloride	500	$CuCl_4$	10
α-cellulose mixture (α-cell 8 parts; vitamins 1 part)	3.0	Nicotinic acid	75	$MnSO_4$	80
		Ca-pantothenate	50	KI	15
		Inositol	200	$CoCl_2$	100/100 g of salt mixture
		Biotin	0.5		
Mineral mix	1.3	Folic acid	1.5		
Water	66.6	Ascorbic acid	100		
		Vitamin B_{12}	10 mcg		
		Menadione (K)	4 mg		
		Alpha-tocopherol acetate (E)	40 mg		
		Beta carotene (A)	2 mg		
		Activated 7-dehydro-cholesterol (D)	5 mcg (per 100-g solids)		

(2) Clark's chinook mash (Moore-Clark Co., Salt Lake City, Utah)

Basic composition	%	Vitamin mix	Mineral mix
Crude protein not less than	55.0	Vitamin A acetate	Manganese sulphate
		Pyridoxine hydrochloride (B_6)	Magnesium sulphate
Crude fat not less than	9.0	Vitamin B_{12} supplement	Iron sulphate
		Ascorbic acid (C)	Iron carbonate
Crude fibre not more than	5.0	D-activated animal sterol	Iron oxide
		Alpha tocopherol (E)	Calcium carbonate
Moisture not more than	10.0	Menadione sodium bisulfite (K)	Copper carbonate
Ash not more than	15.0		Zinc sulphate
Derived from:		Riboflavin (B_2)	Zinc oxide
Fish meal		Choline chloride	Potassium iodide
Animal liver and glandular meal		Thiamine mononitrate	Sodium carbonate
		Niacin	Cobalt sulphate
Dried buttermilk		Inositol	Cobalt carbonate
Blood meal		Calcium pantothenate	(Added mineral matter not more than 3.00%)
Hydrolized poultry feathers		Folic acid	
Condensed fish solubles		Para amino benzoic acid	
Dried fish solubles			
Lecithin			
Fish oil			
Cane molasses			
Ethoxyquin "a preservative"			

(*Continued*)

APPENDIX 1 Ingredients of formulated diets, as supplied by source. — (*Concluded*)

(3) Abernathy moist pellets (Salmon-Cultural Laboratory, Longview, Washington

Basic composition and derivation			Vitamin mix	
	%			
Fish carcass meal	30.0	Salmon, dogfish, hake, herring, or turbot	Thiamin hydrochloride	0.10 g
Dried whey	17.5	No more than 52% lactose (Peebles MNC or equal)	Riboflavin	0.46
			Pyridoxine hydrochloride	0.20
Cottonseed meal	10.8	Not less than 50% protein		
Wheat germ meal	9.4	Not less than 20% protein	Niacin	3.18
Vitamin mix	1.0		DL calcium pantothenate	0.91
Carboxymethyl cellulose (CMC)	1.0	High viscosity	Inositol	9.10
Soybean oil	4.4	Technical grade with .01% BHA and .01% BHT	Biotin	0.02
			Folic acid	0.07
Water	25.9		DL alpha tocopherol acetate (7000 IU)	7.00
			Ascorbic acid	17.00
				38.04 g
			Carboxymethyl cellulose (high viscosity)	415.56
			Total	453.60 g

(4) Vitamin diet fortification mixture (Nutritional Biochemicals Corp., Cleveland, Ohio)

	g/100 lb diet		g/100 lb diet
Vitamin A concentrate (200000 units/g)	4.5	Niacin	4.5
		Riboflavin	1.0
Vitamin D concentrate (400000 units/g)	0.25	Pyridoxine hydrochloride	1.0
		Thiamine hydrochloride	1.0
Alpha tocopherol	5.0	Calcium pantothenate	3.0
Ascorbic acid	45.0		mg/100 lb diet
Inositol	5.0		
Choline chloride	75.0	Biotin	20
Menadione	2.25	Folic acid	90
p-Aminobenzoic acid	5.0	Vitamin B_{12}	1.35

The North and Central American Species of *Rhabdochona* Railliet 1916 (Nematoda: Rhabdochonidae) of Fishes, Including *Rhabdochona canadensis* sp.nov.

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MORAVEC, F., AND H. P. ARAI. 1971. The North and Central American species of *Rhabdochona* Railliet 1916 (Nematoda: Rhabdochonidae) of fishes, including *Rhabdochona canadensis* sp.nov. J. Fish. Res. Bd. Canada 28: 1645–1662.

The systematics of the representatives of the genus *Rhabdochona*, parasitic in fishes of North and Central America, is revised. *Rhabdochona cascadilla* Wigdor 1918, *R. kidderi* Pearse 1936, *R. decaturensis* Gustafson 1949, *R. cotti* Gustafson 1949, *R. ovifilamenta* Weller 1938, *R. milleri* Choquette 1951, and *R. canadensis* sp.nov. are considered as the valid species of this region. The first six species are redescribed and illustrated. The new species, *R. canadensis*, is described from the cyprinids *Hybopsis gracilis* (flathead chub; type host), *H. plumbea* (lake chub), and *Rhinichthys cataractae* (longnose dace) of Alberta; the latter form is characterized largely by the presence of one or two long filaments at each pole of the eggs, by 14 teeth in the prostom, by the presence of the cuticular spike at the tip of the tail, and by the character of the spicules. The species *R. pellucida* Gustafson 1949 is regarded as a synonym of *R. cascadilla* Gustafson 1949, and *R. laurentiana* Lyster 1940 as a synonym of *R. ovifilamenta* Weller 1938. *Rhabdochona serrata* (Wright 1879) Ko and Anderson 1969 is transferred to the genus *Cystidicola* as species inquirenda. The hosts and geographical distribution of the current members of the genus are reviewed. The paper is supplemented by a key for the identification of the species parasitic in fishes of North and Central America.

MORAVEC, F., AND H. P. ARAI. 1971. The North and Central American species of *Rhabdochona* Railliet 1916 (Nematoda: Rhabdochonidae) of fishes, including *Rhabdochona canadensis* sp.nov. J. Fish. Res. Bd. Canada 28: 1645–1662.

Nous passons en revue la systématique des représentants du genre *Rhabdochona*, parasites des poissons de l'Amérique du Nord et de l'Amérique centrale. *Rhabdochona cascadilla* Wigdor 1918, *R. kidderi* Pearse 1936, *R. decaturensis* Gustafson 1949, *R. cotti* Gustafson 1949, *R. ovifilamenta* Weller 1938, *R. milleri* Choquette 1951 et *R. canadensis* nov.sp. sont considérées comme espèces valables de cette région. Nous donnons une nouvelle description, accompagnée d'illustrations, des six premières espèces. Nous décrivons l'espèce nouvelle, *R. canadensis*, provenant des cyprins *Hybopsis gracilis* (le méné à tête plate; hôte type), *H. plumbea* (le méné de lac) et *Rhinichthys cataractae* (le naseux de rapides) d'Alberta; ce dernier parasite est caractérisé surtout par un ou deux longs filaments à chaque pôle de l'oeuf, 14 dents au prostome, un piquant cuticulaire à l'extrémité caudale et la nature des spicules. Nous considérons *R. pellucida* Gustafson 1949 comme synonyme de *R. cascadilla* Gustafson 1949 et *R. laurentiana* Lyster 1940 comme synonyme de *R. ovifilamenta* Weller 1938. Nous transférons *Rhabdochona serrata* (Wright 1879) Ko et Anderson 1969 au genre *Cystidicola* au même titre. Nous passons en revue les hôtes et la répartition géographique des membres actuels du genre. Nous complétons ce travail par une table d'identification des espèces parasites des poissons de l'Amérique du Nord et de l'Amérique centrale.

Received April 1, 1971

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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THIS paper is another in the series concerned with the revision of the genus *Rhabdochona* (see Moravec 1971); this portion includes those species occurring in North and Central American fishes. Eight species assigned, at one time or another, to the genus *Rhabdochona*, are considered from North America, and a single species is known to occur in Central America. In addition to the latter species, *R. kidderi*, an unidentified nematode probably representing a new species in the genus, was recorded by Moravec and Baruš (1971) from Cuba. Many of the earlier descriptions and drawings of these species are inadequate, making an exact identification of the species difficult or impossible; moreover, in recent papers, these nematodes are often designated only as *Rhabdochona* sp. Based on various borrowed materials and on that collected by the second author, we have attempted to make a comparative study that might enable more reliable species identification and might help to form a basis for future work on the biology of these helminths. This review indicates that there are, at present, only seven species in this region that may be considered valid.

The methods used for inspection of the specimens have been described in another paper (Moravec 1971). The names of the hosts and their systematics are after Bailey et al. (1970).

Rhabdochona (*Rhabdochona*) *cascadilla* Wigdor 1918

(Fig. 1)

Syn. — *Rhabdochona pellucida* Gustafson 1949.

The description is based on two of Gustafson's specimens from the U.S. National Museum Helminthological Collection (No. 36993).

Male (*1 worm*) — Body 7.04 mm long, maximum width 0.154 mm. Prostom funnel-shaped, 0.015 × 0.009 mm, basal teeth only slightly outlined. Prostom lined internally with longitudinal thickenings forming at their anterior ends small, forwardly directed teeth; exact number not established. Length of vestibule including prostom 0.069 mm, of muscular oesophagus 0.237 mm, of glandular oesophagus 1.58 mm. Deirids small, bifurcate, 0.063 mm from anterior extermity. Nerve ring encircling oesophagus 0.114 mm from anterior end; excretory pore not located. Ten pairs of preanal papillae present, 9 pairs subventral and 1 pair lateral; lateral pair located at level of third subventral pair (counted from cloaca). Six pairs of postanal papillae present, second pair lateral and remaining pairs subventral. Smaller spicule 0.087 mm long with reflected barb at distal end. Larger spicule 0.321 mm long, anterior end cup-shaped, distal tip indistinct. Length ratio of spicules 1:3.69. Tail conical, 0.240 mm long, with terminal cuticular spike.

Female (*2 fragments of the anterior part of body*) — Body length could not be determined, maximum width 0.198 mm. Prostom without basal teeth, 0.021 × 0.015 mm. Length of vestibule including prostom 0.099 mm, of muscular oesophagus 0.210 mm, of glandular oesophagus 2.97 mm. Distance of deirids from anterior extremity 0.063 mm, of nerve ring 0.144 mm, of excretory pore 0.195 mm. Eggs oval, 0.036–0.042 × 0.024 mm, embryonated, without filaments.

Location — Intestine.

Hosts — According to Wigdor (1918) the type hosts are *Semotiltus atromaculatus* and *Notropis cayuga* (Cyprinidae). However, Choquette (1951) indicates that *N. cayuga* was based on what is known to be *Notropis heterolepis* and *N. bifrenatus* and cites only *Semotilus atromaculatus atromaculatus* as the type host. Gustafson (1949) redescribed this species from specimens from *S. a. atromaculatus* and *Hyborhynchus notatus*. In addition to these hosts, *R. cascadilla* has been reported from many other genera from various fish families.

Distribution — Wigdor (1918) described this species from Cascadilla Creek, a tributary of Lake Cayuga (New York), from where it was also recorded by Choquette (1951). Gustafson (1949) found it in the Embarass River (Illinois). Besides these earlier findings, various authors have reported *R. cascadilla* from many localities in Canada and the USA. The record of this nematode from the gall bladder of *Pimelodella* in Brazil (Hoffman 1967) is evidently erroneous and probably applies to the species *R. acuminata* (see Vaz and Pereira 1934).

Specimen — U.S. National Museum Helminthological Collection (No. 36993), Beltsville, Maryland.

Comments — The original description of *R. cascadilla* given by Wigdor (1918) is incomplete and includes some erroneous data that have already been discussed in the papers by Gustafson (1949) and Choquette (1951). Since Widgor's specimens are not preserved, Gustafson (1949) and Choquette (1951) redescribed this species on the basis of their own materials; the latter determined the neotype and neoallotype, depositing them in the U.S. National Museum Helminthological Collection (No. 47320); however, we were informed by Mr W. W. Becklund that these specimens could not be found in the collection of that museum. Consequently, we studied Gustafson's specimens (No. 36993) designated as *R. eliminata*. Gustafson probably thought of proposing a new species (i.e., *R. eliminata*), but his 1949 work indicates that he considered them to be *R. cascadilla* Wigdor 1918.

We had only the specimens from the museum at our disposal, and, therefore, it was not possible to prepare "en face" preparations nor to dissect the eggs from the uterus to determine the presence or absence of filaments. The eggs, which were observed within the cleared body of the nematode, seemed

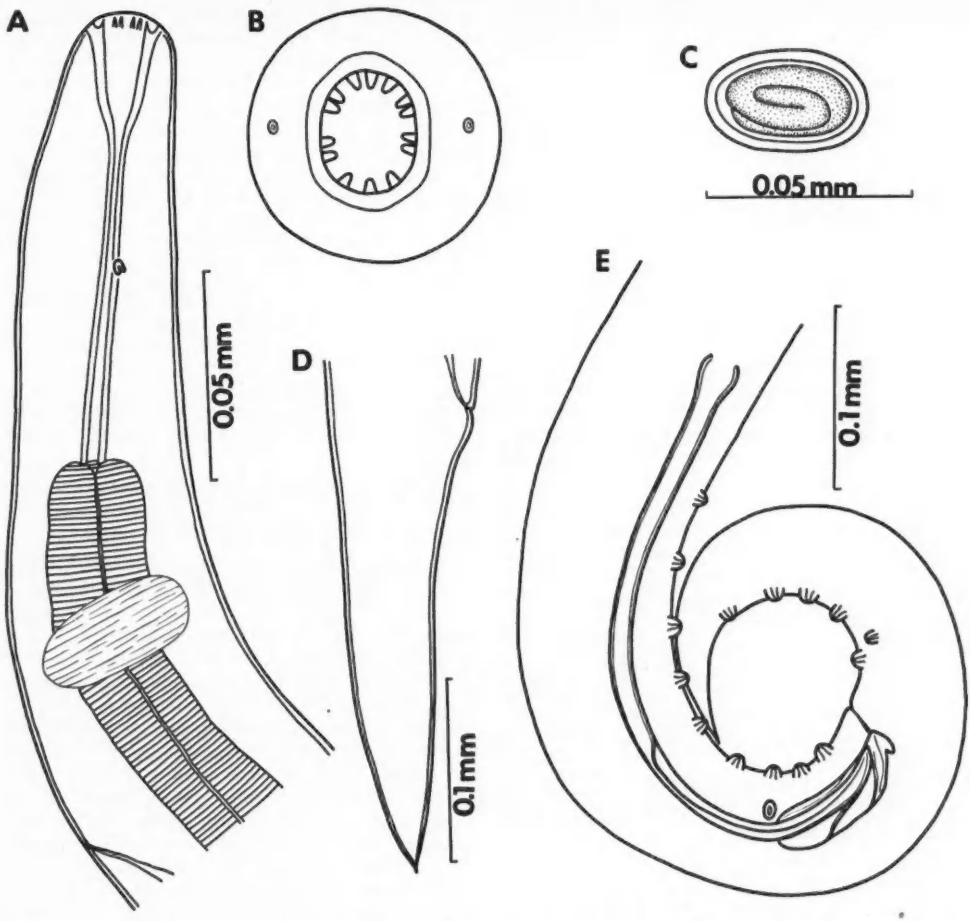

FIG. 1. *Rhabdochona (R.) cascadilla* Wigdor 1918: A, anterior end of female (lateral view); B, anterior end of female (en face view); C, mature egg; D, tail of female (lateral view); E, posterior end of male (lateral view). Orig.

to be smooth and without filaments. However, these features were studied later in specimens from the type host *S. a. atromaculatus* (Turtle River, USA), kindly loaned to us by Dr G. L. Hoffman. We found the number of teeth in the prostom to be 14, and the advanced eggs not filamented.

In 1949, Gustafson described a new species, *Rhabdochona pellucida*, from a fish host, *Ptychocheilus oregonensis* (Cyprinidae), this form being later also reported from the same host by Fritts (1959). However, Rasheed (1965), on the basis of data taken from the literature, synonymized *R. pellucida* with *R. cascadilla*. While studying the only two type specimens (male and female) of *R. pellucida* deposited in the U.S. National Museum Helminthological Collection (No. 36994), we found no substantial differences between *R. pellucida* and *R. cascadilla*. The male of *R. pellucida* exhibits some differences when compared with Gustafson's original description. Our examination indicates: its length is 8.3 mm; spicule lengths of 0.099 and 0.330 mm; subventral preanal papillae arranged asymmetrically (9 papillae on one side and 7 on the other side of the body); subventral postanal papillae arranged asymmetrically (5 papillae on one side and only 3 on the other). Consequently, the size of the body as well as the length of the spicules are practically the same as those of *R.*

cascadilla. It is evident that the number and the arrangement of the subventral papillae show considerable variation, even within the framework of one species, and cannot be used for species differentiation. Since the hosts of *R. pellucida* and *R. cascadilla* belong to the same family (Cyprinidae), we concur with Rasheed's opinion that *R. pellucida* is a synonym of *R. cascadilla*.

The species *R. cascadilla* has been reported by many authors (Anthony 1963; Bangham 1944, 1951, 1955; Bangham and Adams 1954; Bangham and Hunter 1939; Bangham and Venard 1946; Choquette 1951; Fischthal 1945a, b, 1950, 1956; Gustafson 1949; Meyer 1962) from numerous fish hosts belonging not only to the Cyprinidae, but also to the Acipenseridae, Salmonidae, Gasterosteidae, Catostomidae, Centrarchidae, Percidae, Cottidae, and Hiodontidae. It is probable that in many of these instances, various predatory fishes acquire an occasional parasite while feeding on infected fishes. However, the list of hosts suggests that other species were often mistaken for *R. cascadilla* and consequently, at present, it is difficult to determine the actual range of hosts of this nematode. Through the courtesy of Dr G. L. Hoffman, we were able to study some specimens collected by Dr R. V. Bangham; we found that the nematodes reported by him from *Catostomus commersoni* designated as *R. cascadilla* have filamented eggs, thus indicating an incorrect species identification. More detailed studies may prove that only some members of the Cyprinidae serve as hosts of this parasite.

According to Gustafson (1942, 1949), the intermediate hosts of *R. cascadilla* are mayfly nymphs of the genus *Hexagenia*.

Rhabdochona (*Rhabdochona*) *kidderi* Pearse 1936

(Fig. 2)

We examined two specimens from the host *Rhamdia guatemalensis* from Mexico.

Male (*1 specimen*) — Body 5.89 mm long, maximum width 0.054 mm. Prostom relatively small, funnel-shaped, basal teeth only slightly outlined; prostom 0.015 × 0.012 mm. Number of teeth in prostom not determined; after Chitwood (1938) there are 14 teeth. Length of vestibule including prostom 0.090 mm, of muscular oesophagus 0.186 mm, of glandular oesophagus 1.22 mm. Deirids not observed. Nerve ring encircling muscular oesophagus 0.117 mm from anterior extremity; excretory pore at 0.162 mm. Seven pairs of preanal papillae, the third pair (counted from cloaca) lateral and remaining pairs subventral. Six pairs of postanal papillae present, second pair lateral, remaining subventral. Larger spicule conspicuously long (1.080 mm), the blade representing 56% of the entire length. Distal tip of spicule appears bifurcate. Smaller spicule 0.087 mm long with a dorsal barb at distal tip. Length ratio of spicules 1:12.41. Tail conical, 0.186 mm long, ending in a cuticular point.

Female (*1 specimen*) — Body 14.28 mm long, maximum width 0.109 mm. Prostom 0.021 × 0.018 mm, without distinct basal teeth. Length of vestibule including prostom 0.147 mm, of muscular oesophagus 0.315 mm, of glandular oesophagus 2.24 mm. Neither deirids nor excretory pore located. Nerve ring 0.186 mm from anterior extremity. Vulva postequatorial, 6.0 mm from posterior end of body. Mature eggs small, oval, not filamented, 0.027–0.033 × 0.015–0.018 mm. Tail conical, 0.210 mm long, with pointed tip.

Location — Intestine.

Hosts — *Rhamdia guatemalensis depressa*, *R. g. decolor*, and *R. g. stygeae* (Pimelodidae); after Chitwood (1938) also in "*Typhlias*" (*Typhlichthys?*) *pearsi* (?Amblyopsidae).

Distribution — Hitherto recorded only by Pearse (1936) and Chitwood (1938) in fishes from caves and cenotes of the Yucatan Peninsula of Mexico.

Specimen — U.S. National Museum Helminthological Collection (No. 40471 and 42473), Beltsville, Maryland.

Comments — The type specimens of *R. kidderi* had been originally deposited in the collection of the Museum of Zoology, the University of Michigan (No. 321), which was later assigned to the U.S. National Museum Helminthological Collection. According to Mrs M. B. Chitwood (personal communication), Pearse's type specimens could not be located in the Michigan collection. In the U.S. National Museum Helminthological Collection, however, there are paratypes listed as *Rhabdochona rhamdii* from *Rhamdia guatemalensis* in Mexico, which were kindly loaned to us. These specimens were deposited by Pearse in 1936. It is probable that Pearse changed his mind about the name and used *R. kidderi* instead of *R. rhamdii* in his publication. The morphology of these specimens is fully consistent with the existing descriptions and drawings of *R. kidderi*.

Rhabdochona (*Rhabdochona*) *decaturensis* Gustafson 1949

(Fig. 3)

Two paratypes from the U.S. National Museum Helminthological Collection were studied.

Male (*1 specimen*) — Body 13.29 mm long, maximum width 0.132 mm. Pseudolabia rudimentary. Prostom funnel-shaped, 0.018 × 0.015 mm, with distinct basal teeth. Number of anterior prostomal teeth not determined. Length of vestibule including prostom 0.120 mm,

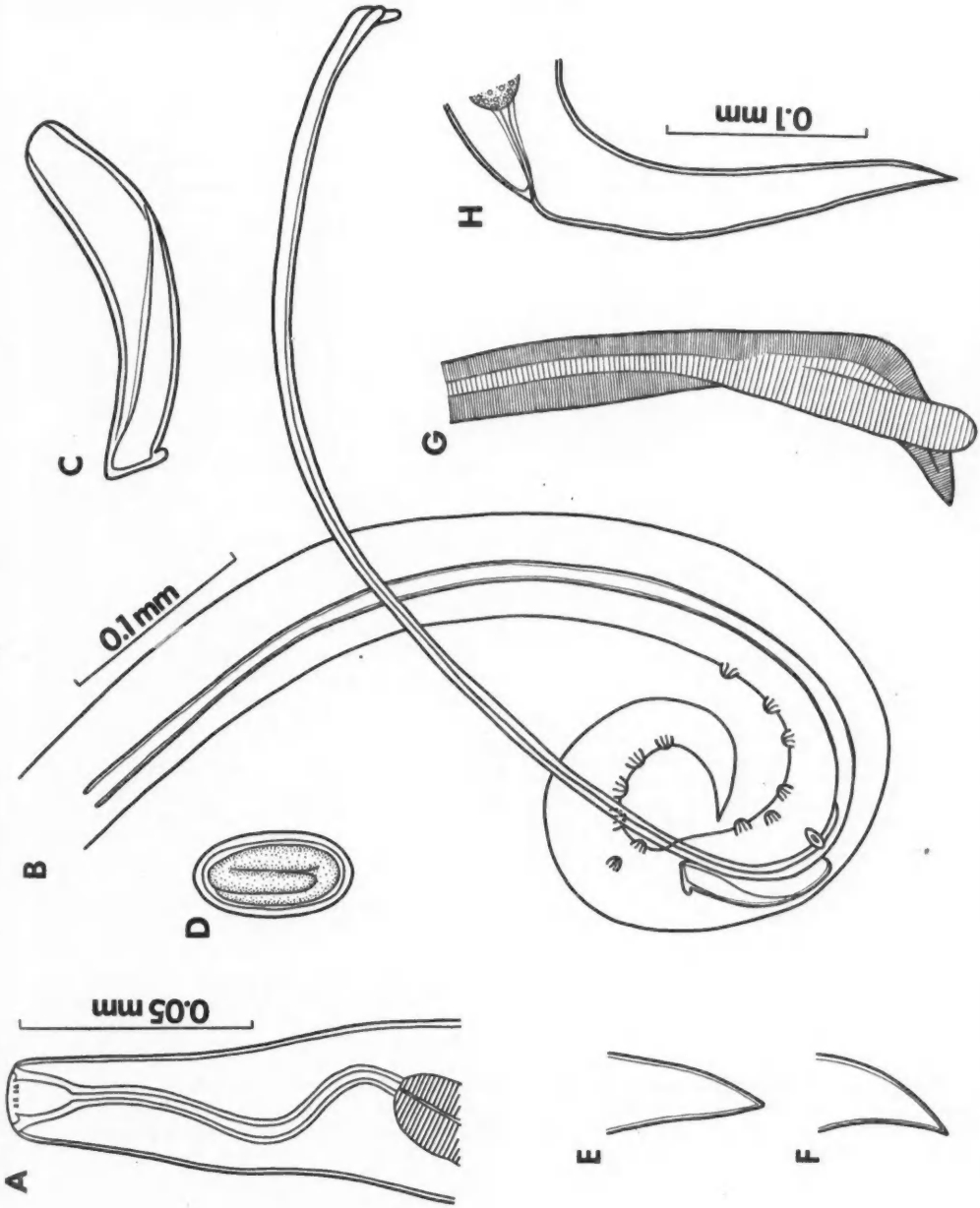

FIG. 2. *Rhabdochona (R.) kidderi* Pearse 1936. A, anterior end of male (lateral view); B, posterior end of male (lateral view); C, smaller spicule D, mature egg; E, tip of female tail; F, tip of male tail; G, distal tip of larger spicule; H, tail of female (lateral view). Orig.

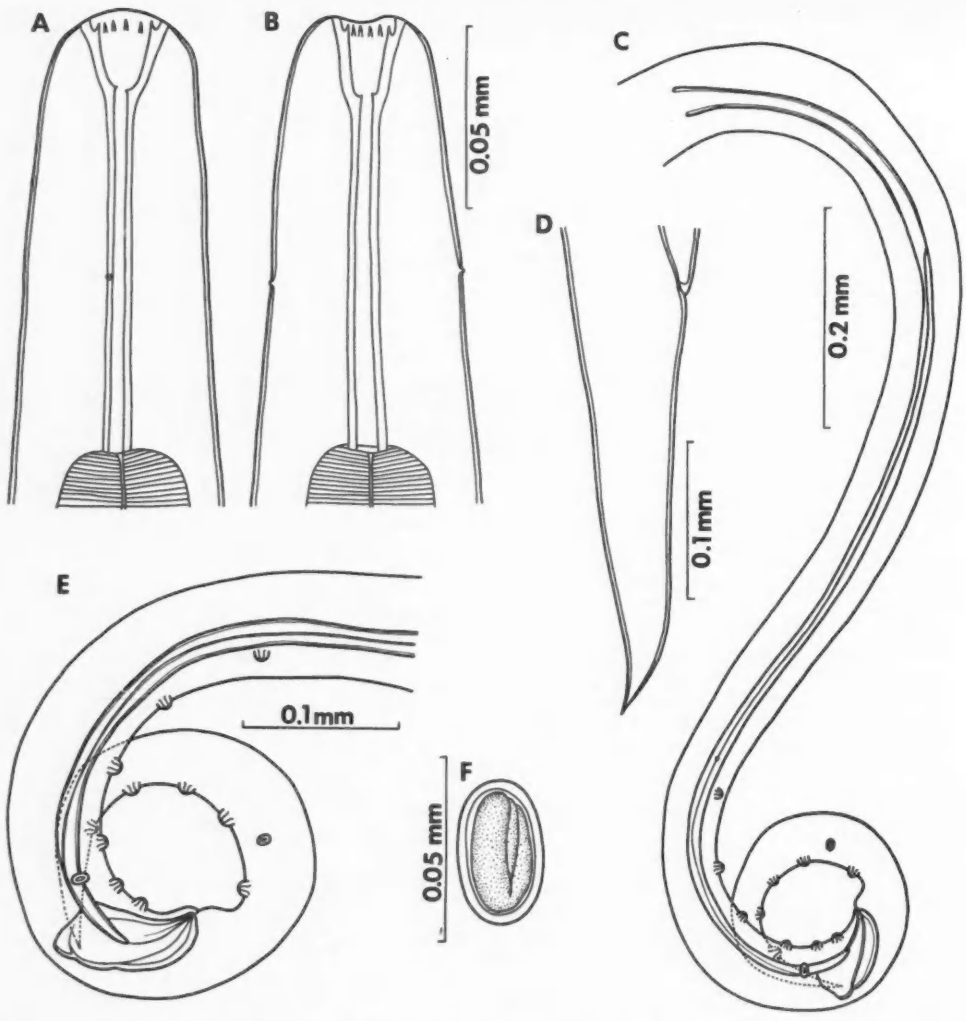

FIG. 3. *Rhabdochona* (*R.*) *decaturensis* Gustafson 1949. A, B, anterior end of female (lateral and dorsal views); C, posterior part of male (lateral view); D, tail of female (lateral view); E, posterior end of male (lateral view); F, mature egg. Orig.

of muscular oesophagus 0.255 mm, of glandular oesophagus 3.52 mm. Deirids very small, simple, approximately opposite to midportion of vestibule. Nerve ring encircling oesophagus 0.180 mm from anterior extremity; excretory pore at 0.273 mm. Seven pairs of preanal papillae present, 6 subventral and 1 lateral. Lateral pair between second and third subventral pairs (counted from cloaca). Six pairs of postanal papillae present, second pair lateral and remaining subventral. Smaller spicule scoop-shaped, 0.090 mm long. Larger spicule very long (1.074 mm), with conical distal tip; spicule shaft representing 73% of entire length. Length ratio of spicules 1:11.93. Tail conical, 0.296 mm long, with terminal cuticular spike.

Female (*1 specimen*) — Body 21.25 mm long, maximum width 0.198 mm. Prostom 0.024 × 0.018 mm. Length of vestibule including prostom 0.120 mm, of muscular oesophagus 0.299 mm, of glandular oesopha-

gus 4.38 mm. Distance of nerve ring 0.183 mm from anterior extremity; of excretory pore 0.270 mm; of small deirids 0.072 mm. Vulva postequatorial, 9.72 mm from posterior end of body. Eggs oval, embryonated, without filaments, 0.039–0.042 mm long, 0.021 mm wide. Tail conical, 0.165 mm long, with terminal cuticular spike.

Location — Intestine.

Hosts — The type host *Aplodinotus grunniens* (Sciaenidae); after Gustafson (1959) less often also in *Ictalurus maculosus* (?); Choquette (1951) gives the hosts *Ictalurus punctatus* (Ictaluridae), *Moxostoma macrolepidotum* (Catostomidae), and *Hiodon tergisus* (Hiodontidae).

Distribution — Recorded by Gustafson (1949) from fishes in Lake Decatur, the Sangamon River, and the Illinois River (all Illinois), and by Choquette (1951) from Tennessee and Wisconsin.

Specimen — U.S. National Museum Helminthological Collection (No. 36992), Beltsville, Maryland.

Comments — Since we studied only the type specimens, it was not possible to determine the exact number of prostomal teeth nor to dissect eggs from the uterus to study their surface. However, in this respect, the data given by Gustafson (1949) seem reliable, since he studied his specimens using "en face" preparations and paid special attention to the presence or absence of egg filaments. According to this author, the eggs of *R. decaturensis* are not provided with filaments, and there are 14 teeth in the prostom.

Morphologically and metrically *R. decaturensis* is very close to *R. kidderi*. According to Gustafson (1949) the latter can be distinguished from *R. decaturensis* mainly by a bifurcate tip of the longer spicule. Unfortunately, this spicule did not protrude out of the body of the male of *R. decaturensis* examined by us and we could not study the tip in detail. The distal tip of the same spicule in *R. kidderi* seemed to be twisted at a right angle and the end of the sheath covering the central part of the spicule shaft bent and, consequently, the distal tip of this spicule acquires a bifurcate appearance. However, both types of nematodes differ distinctly in the length of the shaft of the long spicule; the blade is evidently longer in *R. decaturensis*. Gustafson wrote that the blade of this spicule represents 72–76% and 51–56% of the entire length in *R. kidderi* and *R. decaturensis*, respectively; however, his drawings indicate that these data are erroneous and that the blade is about 41% of the entire length in *R. kidderi*, and in *R. decaturensis* only 31%. It is possible that both nematode types are conspecific and represent two geographical races; however, until these ideas are confirmed by subsequent investigations, it is necessary to consider them as independent species.

According to Gustafson (1939, 1949), the intermediate hosts of *R. decaturensis* are mayflies of the genus *Hexagenia*.

Rhabdochona (*Filochona*) *canadensis* sp.nov.

(Fig. 4,5)

A large number of these nematodes was collected by the second author from various fishes in the province of Alberta. The following description is based on specimens from *Hybopsis gracilis*.

Male (*9 specimens*) (measurements of holotype in parentheses) — Body 5.74–8.36 (8.32) mm long, maximum width 0.109–0.150 (0.122) mm. Pseudolabia rudimentary. Prostom conspicuously wide, funnel-shaped, without basal teeth, 0.015–0.021 (0.021) mm long, maximum width 0.012–0.015 (0.015) mm. Prostom lined internally with 14 longitudinal ribs, forming at their anterior ends small forwardly directed teeth. Vestibule including prostom 0.120–0.165 (0.165) mm long. Length of muscular oesophagus 0.186–0.306 (0.216) mm, of glandular oesophagus 2.18–3.90 (3.90) mm. Nerve ring encircling muscular oesophagus 0.177–0.207 (0.198) mm from anterior end of body; excretory pore at 0.237–0.279 mm (pore not located in holotype). Deirids small, bifurcate, situated slightly anterior to middle of vestibule, 0.051–0.069 (0.069) mm from anterior extremity. Subventral preanal papillae asymmetrical in holotype (9 papillae on one side and 7 on other); in paratypes, the following combinations occurred: 7 + 7, 7 + 9, 8 + 8, and 9 + 9. Additional pair of lateral preanal papillae at level of third subventral pair (counted from cloaca). Six pairs of postanal papillae present: 5 subventral and 1 lateral; latter pair at level of first subventral pair. Smaller spicule 0.102–0.129 (0.126) mm long, with dorsally reflected barb distally. Larger spicule conspicuously slender, 0.471–0.525 (0.495) mm long, with blade representing approximately posterior half. Distal tip of spicule lanceolate thin, with cuticular membrane. Length ratio of spicules 1:3.86–5.14 (1:3.91). Tail conical, 0.270–0.390 (0.390) mm long, with sharp terminal cuticular spike.

Female (*12 specimens*) (measurements of allotype in parentheses) — Body of gravid females 9.88–27.92 (14.85) mm long, maximum width 0.190–0.408 (0.245) mm. Prostom wide, 0.021–0.033 (0.030) mm long, maximum width 0.021–0.027 (0.024) mm. Length of vestibule including prostom 0.144–0.195 (0.186) mm, of muscular oesophagus 0.300–0.510 (0.480) mm, of glandular oesophagus 3.26–5.07 (4.52) mm. Distance of nerve ring from anterior extremity 0.219–0.270 (0.237) mm, of excretory pore 0.351–0.420 (0.369) mm, of deirids 0.063–0.078 (0.072) mm. Tail conical, 0.216–0.309 (0.231) mm long, terminating in a sharp cuticular spike. Vulva postequatorial, 4.27–13.15 (5.90) mm from posterior end of body. Mature eggs oval, embryonated, 0.036–0.042 × 0.018–0.021 mm (0.036–0.042 × 0.018–0.021), with 1–2 long filaments on each pole. Fully mature eggs usually with two filaments on

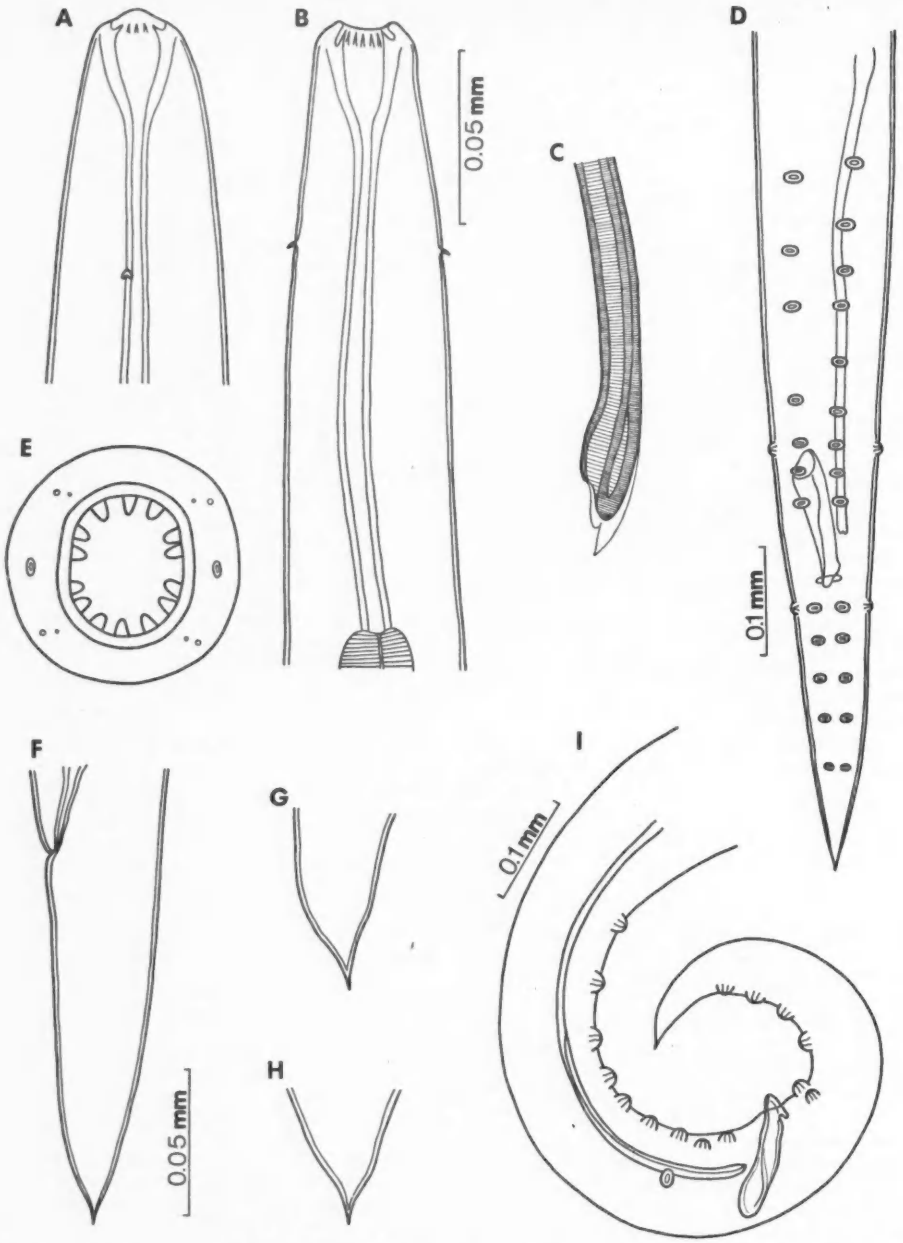

FIG. 4. *Rhabdochona* (*F.*) *canadensis* sp.nov. A, B, anterior end of female (lateral and dorsal views); C, distal tip of longer spicule; D, posterior end of male (ventral view); E, anterior extremity of female (en face view); F, tail of female (lateral view); G, tip of male tail; H, tip of female tail; I, posterior end of holotype male (lateral view). Orig.

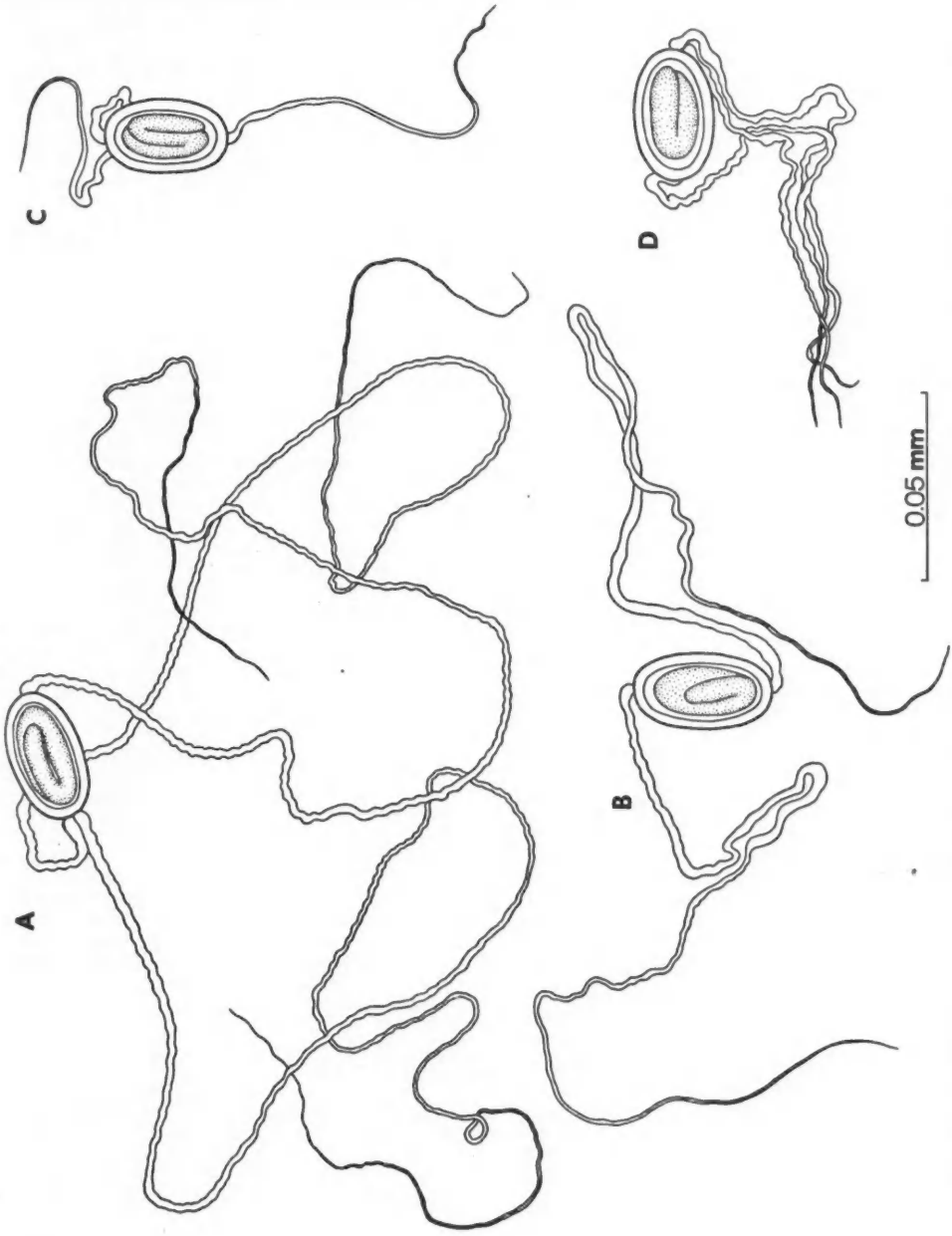

FIG. 5. *Rhabdochona (F.) canadensis* sp.nov. — mature egg. A, B, from *Hybopsis gracilis*; C, D, from *Rhinichthys cataractae*. Orig.

one pole and with only one filament on the opposite pole; however, often two filaments on each pole or only one filament on each pole but greater number of filaments not observed. Filaments very long (about 0.6 mm), with relatively wide base and ends sometimes frayed. If two filaments on one pole, one may be considerably less developed than other. This variability may be due to age of eggs, since in younger eggs, filaments shorter and more slender.

Location — Intestine.

Hosts — *Hybopsis gracilis* (flathead chub; type host), *Hybopsis plumbea*, and *Rhinichthys cataractae* (all Cyprinidae). Macerated specimens of this species were also found in *Stizostedion vitreum vitreum* (Percidae), *Esox lucius* (Esocidae), and *Noturus flavus* (Ictaluridae); the latter fishes are predatory and probably acquired the nematode accidentally while feeding on infected fishes.

Distribution — Alberta; type locality: Milk River, Warner County, Alta., June 27, 1966.

Specimens — Holotype (♂), allotype (♀), 13 paratypes (5 ♂♂ and 8 ♀♀) and all other material deposited in the collection of the National Museum of Natural Sciences (Ottawa, Ont.); two paratypes (♂ and ♀) in the collection of the Institute of Parasitology, Czechoslovak Academy of Sciences, Prague, Czechoslovakia; two paratypes (♂ and ♀) in the U.S. National Museum Helminthological Collection, Beltsville, Maryland (No. 71792); two paratypes (♂ and ♀) in the British Museum (Natural History), London, England.

Comments — The foregoing description of *R. canadensis* sp.nov. is based on specimens from *H. gracilis*. The nematodes from *H. plumbea* and *R. cataractae* exhibit some features that deviate from those of the type host, e.g., the prostom is distinctly narrower, the egg filaments shorter the length of the larger spicule in the only male from *H. plumbea* is 0.429 mm, whereas in the males from *R. cataractae* it ranges from 0.420 to 0.492 mm. However, we regard these differences' as negligible and attribute them to intraspecific variability. Consequently, the nematodes from all three hosts are considered to be conspecific.

In a list of species of the genus *Rhabdochona* to be published (see Moravec 1971), the subgenus *Filochona* Saidov 1953, typified by the presence of egg filaments, is comprised of 19 species. Of these, by its morphology and measurements, the most closely related species to *R. canadensis* sp.nov. appears to be *R. humili* Roytman et Trofimenko 1964, differing from the former largely by the character and number of egg filaments, more numerous subventral preanal papillae in the male, by the arrangement of the teeth in the prostom, and by its geographical distribution. From other members of the subgenus, *R. canadensis* sp.nov. can be distinguished by the character and number of egg filaments, by the shape and size of the prostom, by the size, type, and location of deirids, by the shape of the posterior end of the tail of the female, and by the character of the distal tip of the larger spicule.

Rhabdochona (*Filochona*) *cotti* Gustafson 1949

(Fig. 6)

We examined paratype specimens from the U.S. National Museum Helminthological Collection.

Male (*1 complete specimen and a fragment of the posterior part of the body of another*) — Body 12.76 mm long, maximum width 0.154 mm. Prostom thick-walled, funnel-shaped, relatively narrow, without basal teeth, 0.015 mm long, maximum width 0.009 mm. Number of prostomal teeth not determined. Length of vestibule including prostom 0.093–0.096 mm, of muscular oesophagus 0.252–0.285 mm, of glandular oesophagus 0.87–1.22 mm. Distance of nerve ring encircling muscular oesophagus 0.165–0.195 mm from anterior end of body, of excretory pore 0.216 mm, of small deirids 0.072 mm (situated slightly posterior to middle of vestibule); shape of deirids not determined. Seven–eight pairs of subventral and 1 pair of lateral preanal papillae present; latter pair at level of third subventral pair (counted from cloaca). Six pairs of postanal papillae present with second pair lateral and remaining subventral. Shorter spicule 0.102–0.105 mm long, without distinct barb distally. Larger spicule 0.354–0.357 mm long with distal tip appearing lanceolate and similar to that in *R. canadensis* sp.nov. Length ratio of spicules 1:3.37–3.50. Tail conical, 0.285–0.294 mm long, with distinctly rounded tip, i.e., without usual cuticular spike.

Female (*2 complete specimens and a fragment of posterior part of another*) — Body 19.20–29.48 mm long, maximum width 0.258–0.462 mm. Prostom 0.024–0.027 × 0.012–0.018 mm. Length of vestibule including prostom 0.099–0.111 mm, of muscular oesophagus 0.330 mm, length of glandular oesophagus not determined. Deirids, nerve ring, excretory pore, vulva, and eggs not studied due to poor condition of specimens. Tail conical, 0.210–0.300 mm long, with distinctly rounded tip, without cuticular spike.

Location — Intestine.

Hosts — *Cottus cognatus* (type host), *C. asper*, *C. rhotheus*, and *C. gulosus* (all Cottidae).

Distribution — This species has been recorded by Gustafson (1949) in the Griffith Springs State Fish Hatchery, Spokane, Washington, and in the Little Spokane River and its tributaries (Washington), and by Bangham and Adams (1954) in fishes of British Columbia.

Specimens — U.S. National Museum Helminthological Collection (No. 36991), Beltsville, Maryland.

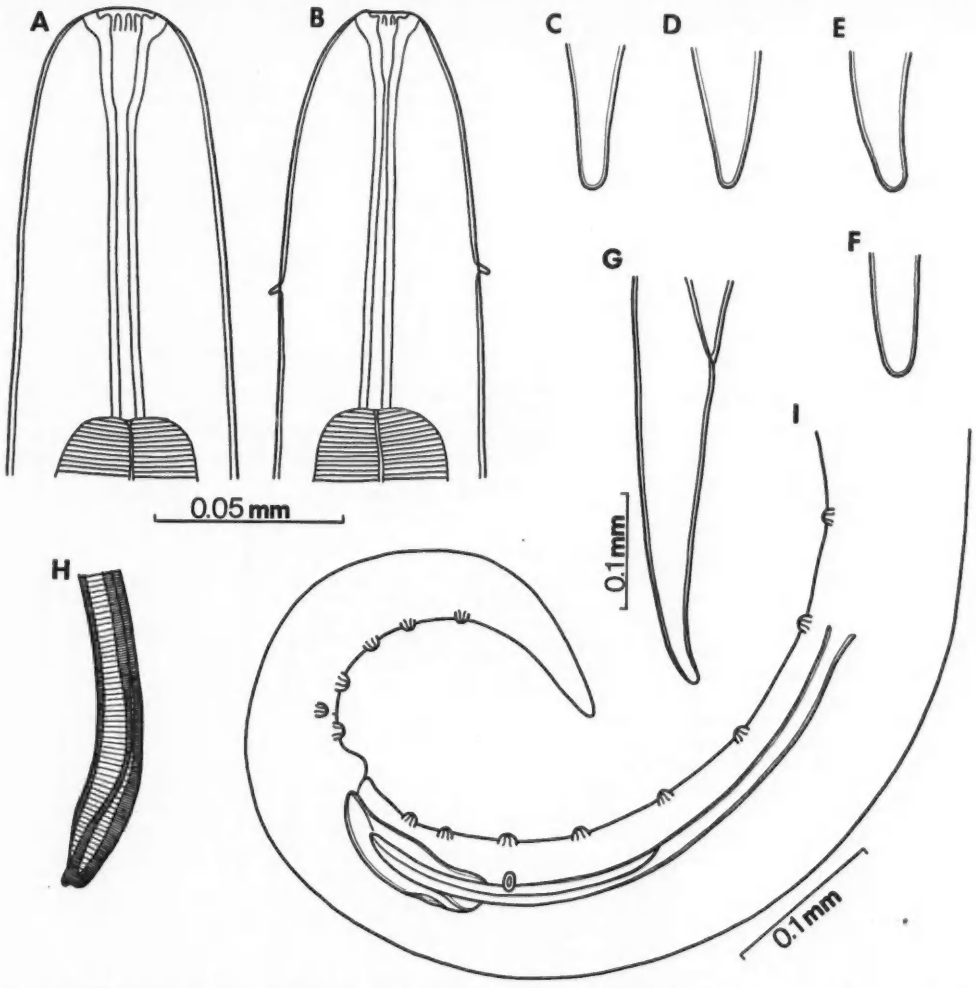

FIG. 6. *Rhabdochona* (*F.*) *cotti* Gustafson 1949. A, anterior end of female (lateral view); B, anterior end of male (dorsal view); C, D, tip of male tail; E, F, tip of female tail; G, tail of female (lateral view); H, approximate shape of distal tip of longer spicule; I, posterior end of male (lateral view). Orig.

Comments — We were not able to study the character of the egg filaments nor to determine the number of teeth in the prostom. However, we consider Gustafson's (1949) data to be reliable. According to this author, there are 14 teeth in the prostom and the eggs are provided with two long single (rarely double) filaments. This species can be easily distinguished from other North American members of this genus by the shape of the tail tip in both sexes.

Rhabdochona (*Filochona*) *ovifilamenta* Weller 1938

(Fig. 7)

Syn. — *Rhabdochona laurentiana* Lyster 1940.

The following description is based on specimens from *Catostomus commersoni* and *C. platyrhynchus* collected by the second author in Alberta.

Male (*3 complete specimens and 3 fragments*) — Body 6.55–8.02 mm long, maximum width 0.095–0.136

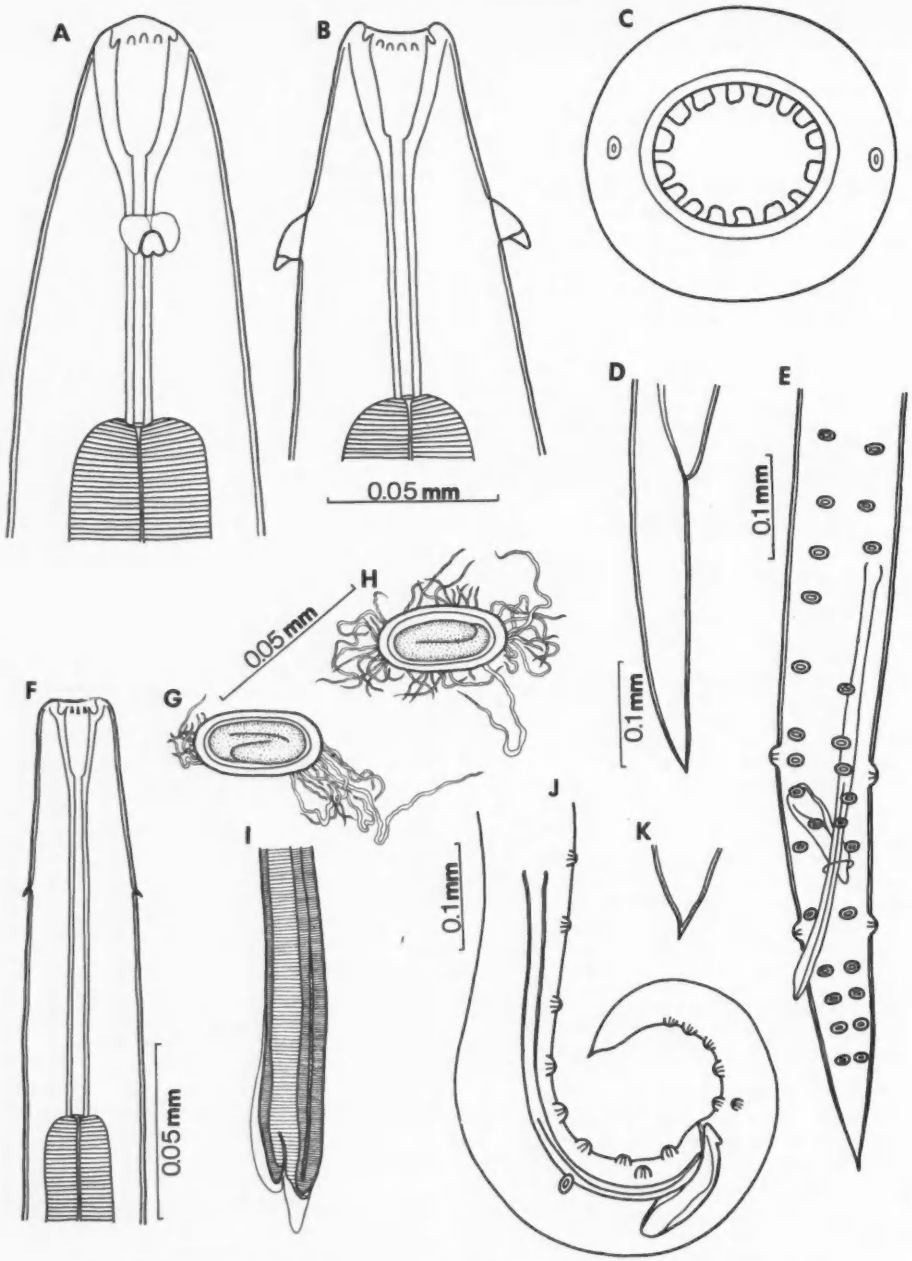

FIG. 7. *Rhabdochona* (*F.*) *ovifilamenta* Weller 1938. A, B, anterior end of female (lateral and dorsal views); C, anterior end of female (en face view); D, tail of female (lateral view); E, posterior end of male (ventral view); F, anterior end of male (dorsal view); G, mature egg from *Catostomus platyrhynchus*; H, mature egg from *Catostomus commersoni*; I, distal tip of longer spicule; J, posterior end of male (lateral view); K, tip of female tail. Orig.

mm. Pseudolabia rudimentary. Prostom relatively narrow, funnel-shaped, with basal teeth only slightly outlined, 0.021–0.024 mm long, maximum width 0.012 mm. Prostom lined internally with ribs, forming at their anterior ends, forwardly directed teeth (exact number not determined). Length of vestibule including prostom 0.111–0.138 mm, of muscular oesophagus 0.255–0.300 mm, of glandular oesophagus 1.90–3.59 mm. Nerve ring encircling muscular oesophagus 0.156–0.204 mm from anterior end of body; excretory pore at a distance of 0.237–0.264 mm. Deirids relatively small, bifurcate, opposite to midportion of vestibule, 0.051–0.078 mm from anterior end. In specimens examined, the following combinations in the number of subventral preanal papillae occurred: 6 + 7, 7 + 9, 8 + 9, 9 + 10. Additional pair of preanal papillae located laterally at level of fourth subventral pair (counting from cloaca). Six pairs of postanal papillae present, second pair lateral and remaining subventral. Smaller spicule scoop-shaped, 0.105–0.117 mm long, with reflected barb at tip. Larger spicule 0.390–0.420 mm long, slender, with lanceolate distal tip, with slightly outlined bifurcation, with fine cuticular membrane. Length ratio of spicules 1:3.52–3.78. Tail conical, 0.303–0.372 mm long, with distinct cuticular spike at tip.

Female (*3 complete specimens and 2 fragments*) — Body 11.75–21.76 mm long, maximum width 0.204–0.258 mm. Pseudolabia rudimentary. Prostom large, thick-walled, with distinct basal teeth, 0.030–0.039 mm long, maximum width 0.012–0.024 mm, with 16 prostomal teeth. Mesostom relatively short. Length of vestibule including prostom 0.090–0.135 mm, of muscular oesophagus 0.276–0.558 mm, of glandular oesophagus 1.60–4.42 mm. Nerve ring 0.126–0.210 mm and excretory pore 0.243 mm from anterior extremity. Deirids relatively large, somewhat bifurcate, near middle of length of vestibule, 0.039–0.060 mm from anterior extremity. Vulva of younger females slightly pre-equatorial; in larger females distinctly postequatorial, 6.23–8.98 mm from posterior end of body. Eggs oval, 0.036–0.042 × 0.018–0.021 mm. Mature eggs embryonated. Entire surface of egg covered with fine protuberances and with numerous, short, threadlike filaments; filaments distributed uniformly over entire surface of majority of eggs, but in some, filaments appear restricted to area near poles. Tail conical, 0.294–0.315 mm long, with short cuticular spike at tip.

Location — Intestine.

Hosts — This species was originally reported by Weller (1938) from *Perca flavescens* (Percidae); however, our materials indicate that *R. ovifilamenta* is more typically a parasite of *Catostomus commersoni* and *C. platyrhynchus* (Catostomidae). We believe that *P. flavescens* probably acquired the parasite while feeding on infected fish. This idea is suggested by the fact that Weller found *R. ovifilamenta* in only a single perch out of a total 655 that he examined. Tedla and Fernando (1969) listed *R. ovifilamenta* as a species from the body cavity of *P. flavescens* taken in the Bay of Quinte, Lake Ontario. Since the form was not treated further in their study, it is assumed that the incidence and intensity of infection were quite low.

Distribution — Hitherto recorded by Weller (1938) from the Straits of Mackinaw (Michigan), Bay of Quinte, Lake Ontario (Ontario) by Tedla and Fernando (1969), and is now reported from Alberta.

Specimens — Deposited in the National Museum of Natural Sciences (Ottawa, Ont.).

Comments — We had the opportunity to compare our specimens of *R. ovifilamenta* from catostomids with the type specimens from *P. flavescens* deposited in the U.S. National Museum Helminthological Collection (No. 9074). We found no substantial differences between the two groups. Unfortunately, the type specimens are preserved as stained preparations mounted in Canada balsam and consequently, due to a high degree of clearing, some structures (e.g., deirids, basal teeth of prostom) are indistinct. We can confirm the observations of Choquette (1951) and of Holloway and Klewer (1969) that the gubernaculum, mentioned in the original description, is absent in these specimens; we have also found that the tail alae in the male are absent as well.

In 1940, a new species, *Rhabdochona laurentiana*, was described by Lyster from *C. commersoni*, which was later synonymized by Choquette (1951) with *R. cascadilla* Wigdor 1918. Lyster's description of *R. laurentiana* is inadequate, drawings are schematic, and the type specimens do not exist. Based on the host species and the length of the larger spicule, we are of the opinion that this species should be regarded as a synonym of *R. ovifilamenta* rather than *R. cascadilla*. The size of the larger spicule in the type of *R. ovifilamenta* is 0.45 mm, and that of *R. laurentiana* was given to be about 0.5 mm. In addition, *R. cascadilla* appears to be a parasite more typical of cyprinids, whereas both *R. ovifilamenta* and *R. laurentiana* have been reported from catostomid fishes.

Weller (1938) experimentally infected the amphipod, *Hyalella knickerbockeri*, with eggs of *R. ovifilamenta*; however, this report appears to be unreliable, since the morphology of the larvae recovered from the crustacean corresponds to representatives of the Tylenchata, indicated by the presence of a stylet.

Rhabdochona (*Filochona*) *milleri* Choquette 1951

(Fig. 8, 9)

The following description is based on specimens from *Moxostoma macrolepidotum* (=*M. aureolum*) from the

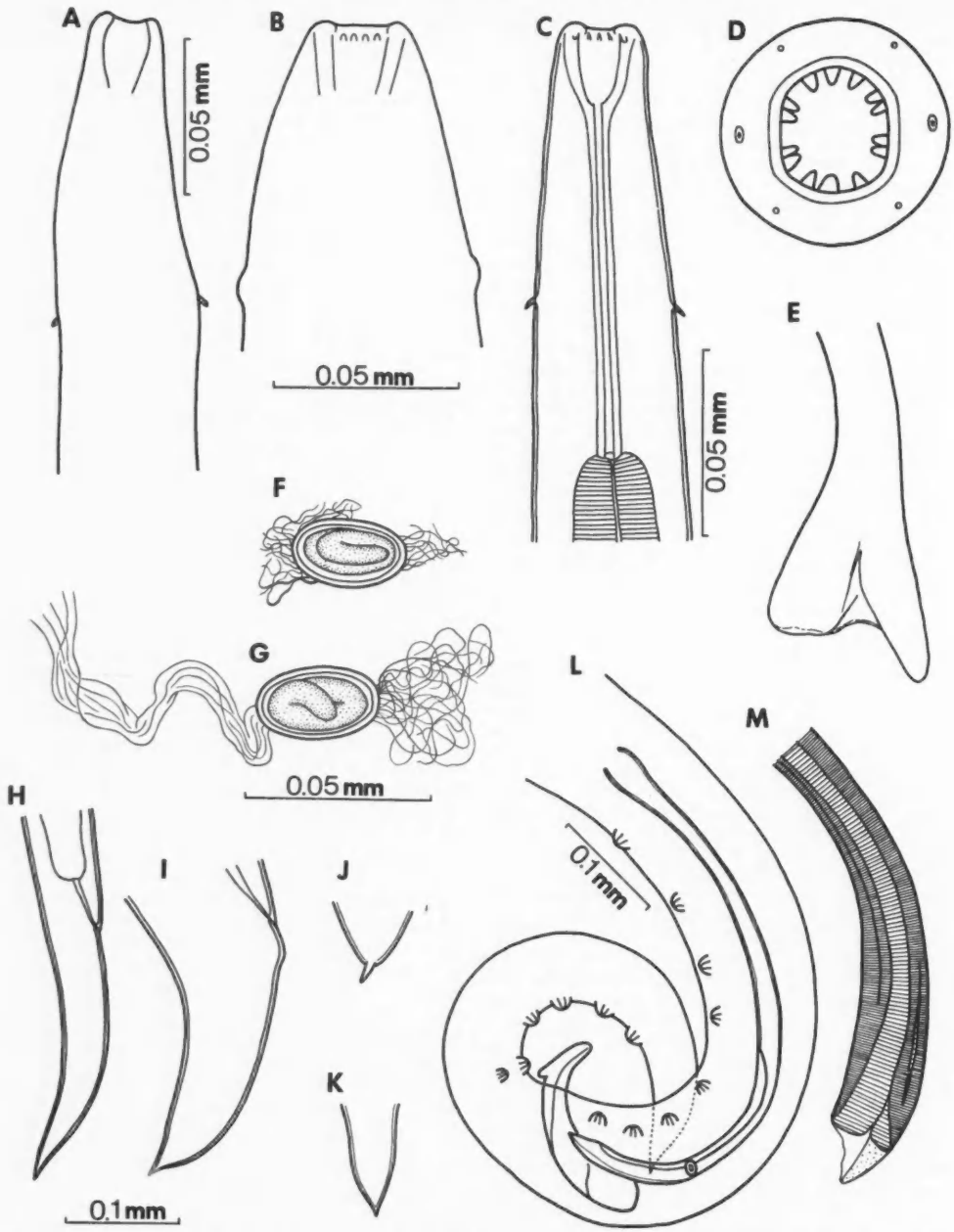

FIG. 8. *Rhabdochona* (*F.*) *milleri* Choquette 1951. A, B, outlines of anterior ends of type specimens (dorsal views); C, anterior end of female (dorsal view); D, anterior end of female (en face view); E, outline of tip of longer spicule of type specimen; F, G, mature eggs; H, tail of female; I, tail of female (type specimen); J, tip of female tail (type specimen); K, tip of female tail; L, posterior end of male (lateral view); M, distal tip of longer spicule. Orig.

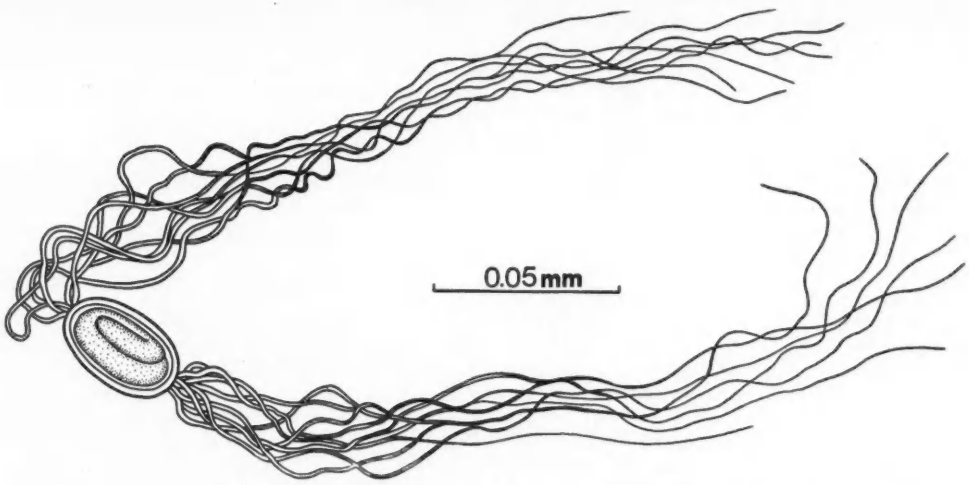

FIG. 9. *Rhabdochona* (*F.*) *milleri* Choquette 1951 — mature egg from *Moxostoma erythrurum*. Orig.

Shenandoah River (USA) obtained from Dr G. L. Hoffman.

Male (*1 specimen*) — Body 6.94 mm long, maximum width 0.176 mm. Prostom funnel-shaped, with distinct basal teeth, 0.018 mm long, maximum width 0.012. Prostom lined internally with longitudinal ribs, forming forwardly directed teeth at their anterior ends; their exact number not determined. Length of vestibule including prostom 0.144 mm, of muscular oesophagus 0.300 mm, of glandular oesophagus 1.36 mm. Nerve ring encircling muscular oesophagus, 0.168 mm from anterior extremity; excretory pore at a distance of 0.237 mm. Deirids small, bifurcate, 0.063 mm from anterior end. Eight pairs of subventral and 1 pair of preanal papillae present; latter pair near level of third subventral pair (counted from cloaca). Of 6 pairs of postanal papillae, 5 pairs subventral and 1 pair lateral at level of first subventral pair. Larger spicule 0.402 mm long, with relatively blunt distal tip, with slightly outlined bifurcation. Smaller spicule 0.129 mm long, with dorsal barb at distal end. Length ratio of spicules 1:3.12. Tail conical, 0.300 mm long, with sharp cuticular spike at tip.

Female (*3 specimens*) — Body 10.91–12.10 mm long, maximum width 0.136–0.163 mm. Prostom funnel-shaped, 0.021–0.024 mm long, 0.015–0.018 mm wide, with distinct basal teeth; 14 teeth in prostom, with lateral teeth arranged in pairs. Length of vestibule including prostom 0.111–0.138 mm, of muscular oesophagus 0.270–0.297 mm, of glandular oesophagus 1.59–2.35 mm. Nerve ring 0.186–0.189 mm and excretory pore 0.261 mm from anterior extremity. Deirids of medium size, bifurcated, 0.063–0.081 mm from anterior end of body. Vulva slightly postequatorial, 5.03–6.12 mm from posterior extremity. Eggs oval, 0.030–0.036 × 0.018–0.021 mm. Surface of advanced eggs (containing larvae) smooth; poles provided with numerous fine filaments; filaments on one pole of egg arranged mostly in parallel, giving an appearance of a short ribbonlike filament with the end frayed; filaments on opposite pole form an irregular cluster. The arrangement of filaments on eggs from some females is similar to that in *R. ovifilamenta* and lateral filaments appeared to be present as well; however, these filaments appear finer than those in the foregoing species. During manipulation it was found that the eggs lose their filaments quite easily. Tail conical, 0.210–0.243 mm long, with sharp cuticular point at end.

Location — Intestine.

Hosts — In *Moxostoma macrolepidotum* (= *M. aureolum*) (type host) and *M. erythrurum* (Catostomidae).

Distribution — Hitherto recorded by Choquette (1951) from the Ottawa River (Quebec, Que.), by Dr G. L. Hoffman (unpublished data) from the Shenandoah River (USA), and by Dr A. Dechtiar (unpublished data) from Lake Erie (Ontario).

Specimens — Collection of Dr G. L. Hoffman, Eastern Fish Disease Laboratory, Leetown (Kearneysville), West Virginia.

Comments — Choquette (1951), describing *R. milleri*, distinguished it from the remaining members of the genus *Rhabdochona* largely by the bifurcation of the longer spicule tip. We examined Choquette's type specimens, which are deposited in the collection of the Institute of Parasitology, MacDonald College, McGill University, Montreal, Que.; however, these specimens proved practically unfit for study. They are fragmented, and, after years,

have become totally black, so that many important features cannot be studied at all. The distal tip of the larger spicule is also blackened; however, it seems to be bifurcate. On comparing this spicular tip of the type specimen with that of the male borrowed from Dr G. L. Hoffman, it appears that they are of the same nature; it is probable that the distal tip of this species may be opened widely, thus assuming a shape ranging from one that is almost pointed to one that is widely bifurcate. In other discernible features the type specimens seem identical to those from the USA.

Through the courtesy of Dr A. Dechtiar we were able also to examine several specimens of this species from the host *Moxostoma erythrurum* obtained in Lake Erie (Ontario). The morphology of these nematodes was practically the same as that from *M. macrolepidotum*, except that the egg filaments were much longer (up to 0.3 mm); these were arranged in two polar tufts, each composed of numerous fine filaments; no lateral filaments were observed. The spicules of males measured 0.405–0.456 and 0.111–0.126 mm, and the subventral preanal papillae occurred in the following combinations: 7 + 8, 8 + 8, 8 + 9, and 8 + 10. All these differences are, however, negligible, and may be due to age or host variability.

In many important features *R. milleri* resembles *R. ovifilamenta*, and subsequent detailed studies might prove their conspecificity; also, the hosts of both species belong only to the family Catostomidae. The more substantial differences are found only in the females: in the size of deirids and the number of teeth in the prostom. However, it is possible that these differences depend only on the age of the nematode and that in older females the deirids become more sizeable and an additional dividing of two teeth in the prostom (one dorsal and one ventral) may take place. These changes are also suggested by the fact that we found only 14 teeth in the prostom of unidentified females (with immature eggs) from *C. commersoni* (Algonquin Park lakes, Ontario) kindly loaned to us by Dr A. Dechtiar. Until further observations are available in this respect, it is necessary to consider the two types of nematodes as independent species.

Species Formerly Assigned to *Rhabdochona*

Rhabdochona serrata

(Wright 1879) Ko et Anderson 1969

Syn. — *Ancyracanthus serratus* Wright 1879; *Cystidicola serratus* (Wright 1879) Railliet 1916.

Location — Auricle.

Host — *Coregonus clupeaformis.*

Distribution — Type locality not given.

Specimen — U.S. National Museum Helminthological Collection (No. 7609).

Comments — The type specimen cannot be located in the U.S. National Museum Helminthological Collection. Wright (1879) found only one female with immature eggs. Pearse (1924) assigned to this species the nematodes collected from *Aplodinotus grunniens* from Lake Repin (Wisconsin) and gave a more detailed description. Later, on the basis of Pearse's redescription, Ko and Anderson (1969) transferred this species to *Rhabdochona* as species *inquirenda*. Considering the host given and the location, it seems probable that the specimen described by Wright (1879) belongs to a species different from that found by Pearse (1924). Although Pearse's forms can be referred to the genus *Rhabdochona*, the specimen described by Wright (1879) is rather a member of *Cystidicola*. Therefore, we suggest that this species be retained as *Cystidicola* species *inquirenda*.

Key to the North and Central American Species of *Rhabdochona* Parasitic in Fishes

1. Mature eggs (containing larvae) without filaments 2
   Mature eggs provided with filaments 4
2(1). Larger spicule shorter than 0.5 mm; length ratio of spicules 1:3.6–5.0 ..... *R. cascadilla*
   Larger spicule much longer than 0.5 mm; length ratio of spicules 1:10.2–13.2 3
3(2). Blade of larger spicule representing about 56% of the entire spicular length; distal tip of spicule bifurcated ..... *R. kidderi*
   Blade of larger spicule representing about 73% of the entire spicular length; distal tip of spicule not bifurcated ..... *R. decaturensis*
4(1). Mature eggs provided with 1–2 long thin filaments at each pole; prostom without basal teeth; parasitic in Cyprinidae or Cottidae 5
   Mature eggs provided with numerous, fine filaments; sometimes the filaments on one pole may be arranged in parallel so that they may assume the appearance of a short ribbonlike filament with

a frayed end; lateral filaments may be present; prostom with basal teeth; parasitic in Catostomidae 6

5(4). Length of larger spicule 0.309–0.370 mm, length ratio of spicules 1:3.37–3.50; smaller spicule without reflected terminal barb; prostom narrow; tail tip of both sexes rounded, without cuticular spike; parasitic in Cottidae..... *R. cotti*
Length of larger spicule 0.471–0.525 mm; length ratio of spicules 1:3.86–5.14; smaller spicule provided with a reflected terminal barb; prostom wide; tail tip of both sexes provided with a sharp cuticular spike; parasitic in Cyprinidae..... *R. canadensis*

6(4). Deirids of gravid females conspicuously large; prostom with 16 teeth..... *R. ovifilamenta*
Deirids of gravid females of medium size; prostom with 14 teeth..... *R. milleri*

Acknowledgments

We express our appreciation to the following who sent us specimens and thus made the present work possible: Mr W. W. Becklund and Mrs M. B. Chitwood, National Animal Parasite Laboratory (U.S. Department of Agriculture), Beltsville, Maryland; Dr K. G. Davey, Institute of Parasitology, Macdonald College, McGill University, Montreal, Que.; Dr G. L. Hoffman, Eastern Fish Disease Laboratory, Leetown (Kearneysville), West Virginia; and Dr A. Dechtiar, Research Branch, Ontario Department of Lands and Forests, Maple, Ont. For help in securing specimens and for providing us with needed literature, we are also indebted to: Dr J. R. Adams, Department of Zoology, University of British Columbia, Vancouver, B.C.; Dr L. P. E. Choquette, Pathology Section, Canadian Wildlife Service, Ottawa, Ont.; and Prof H. W. Manter, Department of Zoology, University of Nebraska, Lincoln, Neb. This work was supported in part by grants to the second author from the National Research Council of Canada and the National Museum of Natural Sciences (Canada).

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NOTES

Offshore Distribution of Pacific Herring (*Clupea pallasi*) on Basis of Records from Fur Seal Stomachs

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TAYLOR, F. H. C. 1971. Offshore distribution of Pacific herring (*Clupea pallasi*) on basis of records from fur seal stomachs. J. Fish. Res. Bd. Canada 28: 1663–1665.

An examination of stomachs of fur seal (*Callorhinus ursinus*) taken off the coast of southern British Columbia and Washington from 1958 to 1969 indicated that Pacific herring (*Clupea pallasi*) were confined mainly to the continental shelf. Herring were most numerous in fur seal stomachs off Barkley Sound. Few occurred north of Cape Cook or from Cape Flattery south to the Columbia River. None were found from seals taken near the Cobb Seamount.

TAYLOR, F. H. C. 1971. Offshore distribution of Pacific herring (*Clupea pallasi*) on basis of records from fur seal stomachs. J. Fish. Res. Bd. Canada 28: 1663–1665.

L'examen d'estomacs d'otaries à fourrure (*Callorhinus ursinus*) capturées au large des côtes du sud de la Colombie britannique et de l'Etat de Washington de 1958 à 1969 indique que le hareng du Pacifique (*Clupea pallasi*) est confiné surtout au plateau continental. Les estomacs contenant le plus grand nombre de harengs provenaient des otaries du détroit de Barkley. Nous en avons trouvé peu au nord du cap Cook ou depuis le cap Flattery au sud jusqu'au fleuve Columbia. Les estomacs d'otaries capturées près du mont sous-marin Cobb ne contenaient pas de harengs.

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THE distribution of Pacific herring (*Clupea pallasi*) is well known when they are concentrated in the coastal channels and inlets during the main fishing season (September–March), or during the spawning season (February–April) (Taylor 1964). Although some herring remain inshore throughout the year, the majority apparently move offshore after spawning (Taylor 1964). Most of the existing information on offshore distribution has been provided by limited summer fisheries. Like these fisheries, most of the other offshore commercial fisheries in British Columbia are confined to the coastal banks. They thus provide little opportunity for gaining additional information on the offshore distribution of herring. In recent years, however, one herring predator, the northern fur seal (*Callorhinus ursinus*), has been taken in numbers for research purposes over an area that extends beyond the coasts of southern British Columbia and the State of Washington. Canada, under the Interim Convention for Conservation of North Pacific Fur Seals, is obligated to take pelagically 500–700 fur seals annually. Although hunting tended to be concentrated in areas where seals were most abundant, and hence, where probably seal food was also abundant, the cruises were continued, in some years at least, far to seaward to establish the offshore limits of the migrating fur seal population.

The surveys from 1958 to 1969 (Fig. 1) showed that most fur seals sighted were in a band 20–50 miles wide, defined by the continental shelf (outer boundary at 100 fath). The greatest concentration (up to 276/10 min square) was off Barkley Sound and the Juan de Fuca Strait. Small numbers of seals were found in a band about twice this distance offshore, with scattered seals encountered to the offshore limit of the survey (about 250 miles from shore). Beyond the limits of the continental shelf, fur seals were found in concentrations above the minimum only in the vicinity of the Cobb Seamount (up to 25/10 min square).

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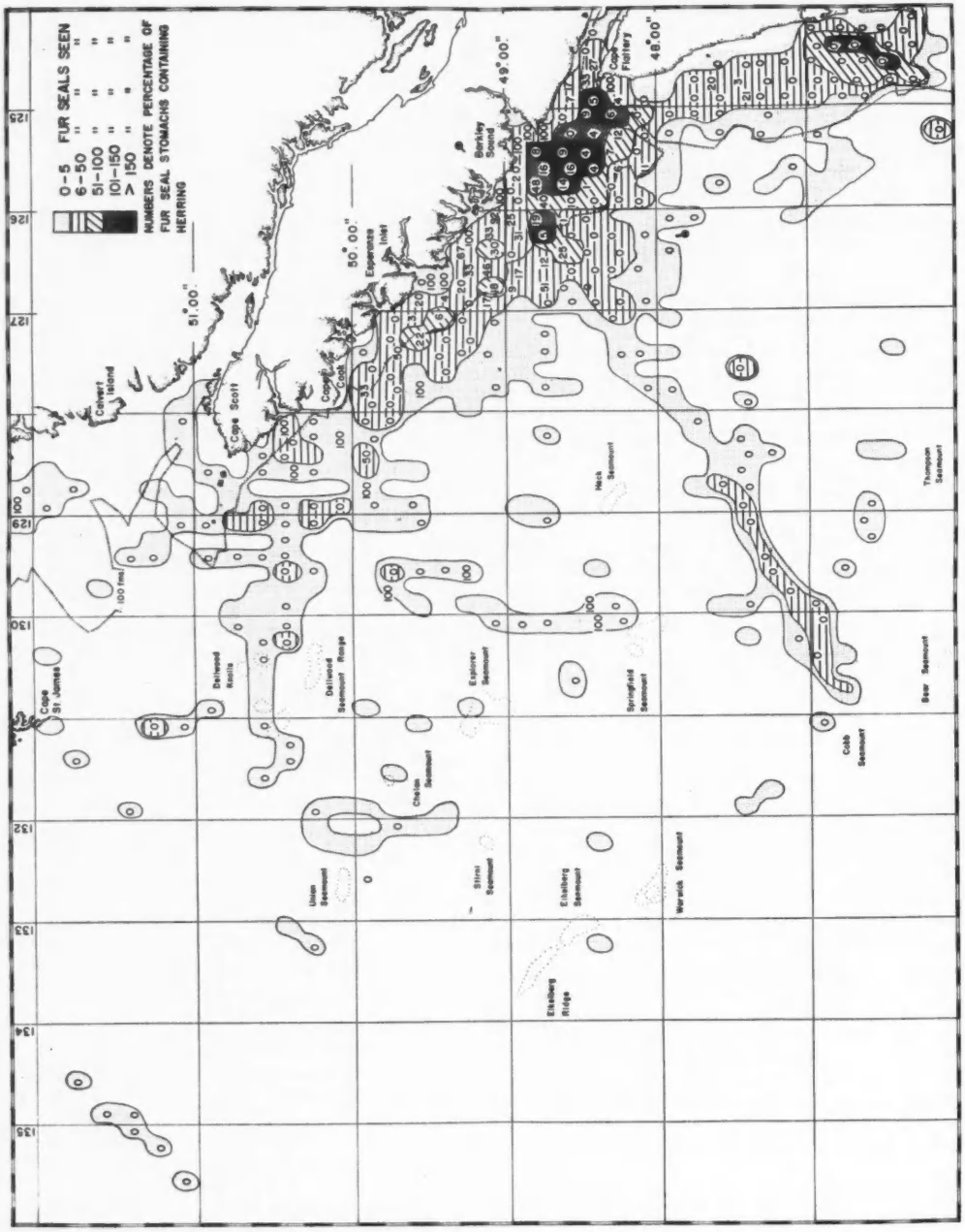

FIG. 1. The distribution of fur seals sighted in five abundance categories by 10-min squares of latitude and longitude, showing the percentage of stomachs that contained herring.

Since fur seals feed extensively on fish and squid, probably selecting those forage species that are most readily available (Taylor et al. 1955), herring, if present in reasonable numbers, could be expected to occur in fur seal stomachs. Herring were not found in the stomachs throughout the whole area, but occurred mainly in those taken over the continental shelf from Cape Flattery north to Esperanza Inlet. They were present in greatest numbers, although not necessarily in the greatest proportion of the stomachs examined, near the southeast and southwest corners of La Pérouse Bank (off Barkley Sound). This is the same area in which in 1968, 1969, and 1970 surveys of the offshore distribution of herring showed herring to be most abundant (Taylor MS 1969, MS 1970; Taylor et al. MS 1970a, b, c, d). Over the continental shelf, from Cape Flattery south to the mouth of the Columbia River, and also from Cape Cook north, herring were infrequently found in fur seal stomachs. Beyond the edge of the continental shelf there were only 11 instances of herring occurring in fur seal stomachs. Nine of these, seven from within 10 miles of the edge of the shelf, and two from 25 to 35 miles outside it, could have been of herring eaten on or near the shelf. The remaining two instances were from seals taken 80–100 miles from the continental shelf and could be the result of faulty identification of fish remains, or of errors in recording position. No herring were found in fur seals from the concentration near the Cobb Seamount.

The occurrence in fur seal stomachs suggests that herring are confined to the continental shelf and are most numerous off southern British Columbia in the vicinity of La Pérouse Bank. North of Cape Cook and south of Cape Flattery to the Columbia River, few herring were found. Only scattered and perhaps doubtful instances of herring in fur seal stomachs occurred at any distance from the continental shelf.

Acknowledgments — I am indebted to the late Mr G. Pike and to Mr I. MacAskie for making the fur seal records available. Mr MacAskie was also responsible for the exacting task of identifying the contents of the fur seal stomachs. I also extend my thanks to Mr A. Rigby, who, shortly before his retirement, was responsible for most of the compilation of the data and for draughting the original figure, later modified by Mr L. W. Barner.

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Derzhavin's Biostatistical Method of Population Analysis[1]

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RICKER, W. E. 1971. Derzhavin's biostatistical method of population analysis. J. Fish. Res. Bd. Canada 28: 1666–1672.

Derzhavin's biostatistical method, as modified by Boiko and others, uses annual age censuses and catch statistics to compute the utilized stock (virtual population), V_i, of year-class *i* in a given year as the sum of all members of that year-class that are caught in the current and future years. The sum of V_i values for all year-classes present in a given year is the total utilized population, V. The biostatistical rate of exploitation for individual ages (C_i/V_i), or for the stock as a whole (C/V), is the catch divided by the utilized stock. If ages of the fish in the stock are read too low, values of C_i/V_i and C/V are too large. For fully recruited fish, C_i/V_i is an unbiased estimate of the total mortality rate, A, but for incompletely recruited ages, it differs progressively from A and has no simple interpretation. Variations in abundance of successive year-classes do not affect the interpretation of C_i/V_i or C/V for fully recruited ages, but changes in rate of fishing, F, are disturbing. When incompletely recruited ages are included in a biostatistical computation (as has usually been done), C/V does not have any precise interpretation in terms of population parameters. In addition, variations in year-class strength affect the value of C/V even when F does not change from year to year. It is possible to use C/V for the whole catch as an "arbitrary" index that reflects the direction and magnitude of changes in intensity of fishing over a period of years. However, even for this purpose the same minimum age must be used in all years. When data for a long series of years are available, the utilized year-class strength (ΣC_i) of the year-class hatched in year *i* can be compared with the total utilized stock (or the utilized mature stock) present in year *i*, in order to examine parent–progeny relations. Incompletely recruited as well as fully recruited ages can be used in this comparison, but adjustments are necessary if mortality rate (natural or fishing) changes from year to year. The biostatistical method does not provide separate estimates of natural and fishing mortality rates. If the possibility of a moderate or large natural mortality is disregarded, serious errors of interpretation may result.

RICKER, W. E. 1971. Derzhavin's biostatistical method of population analysis. J. Fish. Res. Bd. Canada 28: 1666–1672.

La méthode biostatistique de Derzhavin, modifiée par Boiko et autres, se base sur les recensements annuels d'âge et les statistiques de capture pour évaluer le stock utilisé (population virtuelle), V_i, de classe d'âge *i* une année donnée, et comprenant tous les membres de cette classe d'âge capturés pendant l'année courante et les années à venir. Le quotient capture/stock utilisé représente le taux biostatistique d'exploitation d'une classe d'âge particulière (C_i/V_i) ou du stock entier (C/V). Si les poissons sont affectés à une classe d'âge trop basse, les quotients C_i/V_i et C/V sont trop grands. Dans le cas de poissons pleinement recrutés, le quotient C_i/V_i donne un estimé impartial du taux de mortalité totale, A. Dans le cas de poissons partiellement recrutés, ce quotient s'éloigne progressivement de A et ne peut être facilement interprété. Les fluctuations de l'abondance de classes d'âge successives n'affectent pas l'interprétation des quotients C_i/V_i ou C/V, mais les variations du taux de pêche, F, présentent une source d'erreur. Si on introduit des âges partiellement recrutés dans les calculs biostatistiques (comme on l'a fait généralement), C/V n'a plus de signification précise comme paramètre de la population. De plus, le quotient C/V est affecté par les fluctuations de l'abondance des classes d'âge, même si F ne change pas d'une année à l'autre. On peut employer C/V pour la prise entière comme indice "arbitraire" de la direction et de l'amplitude des changements de l'intensité de la pêche au cours des années. Même pour cela, on doit toutefois utiliser le

[1]A Russian version of this paper appeared in 1970 in Rybnoe Khozyaistvo, 46(10): 6–9; 46(11): 5–7, under the title "Biostatisticheskii metod A. N. Derzhavina."

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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même âge minimal pour toutes les années. Si l'on possède des données couvrant une longue période, on peut comparer l'abondance de la classe d'âge utilisée (ΣC_i) à même la classe d'âge éclose au cours de l'année *i* au stock total (ou stock adulte utilisé) de l'année *i*, afin d'étudier les rapports parents–progéniture. Les classes d'âge partiellement et pleinement recrutées peuvent servir à cette comparaison, mais on doit faire certains ajustements si les taux de mortalité naturelle ou par pêche varient d'une année à l'autre. Il est impossible de calculer séparément par la méthode biostatistique les taux de mortalité naturelle et de mortalité par pêche. Si on ne tient pas compte de la possibitité d'une mortalité naturelle modérée ou abondante, on risque de sérieuses erreurs d'interprétation.

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THE term "biostatistical method" or "method of biostatistics" was originally used to designate any type of analysis in which catch statistics of a fish stock are combined with biological information, particularly size-composition, age-composition, and rate of growth. However, in recent years there has been a tendency to limit the term to a particular type of analysis associated with the name of the late Professor A. N. Derzhavin. Actually, the method developed gradually. It was foreshadowed in a paper on the Caspian bream by Tereshchenko (1917), who had been in consultation with Baranov; and a similar computation is given in Baranov (1918). However, the decisive step was taken in 1922 by Derzhavin in his well-known monograph on the Kura River stellate sturgeon.

The method has been described by Ricker (1958 Chapter 8). From representative samples taken over a series of years, the mean age structure of the commercial catches is determined and is used to estimate the number of fish of each year-class present in successive years. Then, an estimate of the *minimum* commercial stock on hand in a given year is obtained by adding up all the fish *of the year-classes represented in that year's catch* that are caught in subsequent years. This estimate is called the "utilized stock" (izpol'zuemyi zapas) by Voevodin (1938). It is a minimum estimate of the total stock because fish that die naturally are not included in it.

Derzhavin worked with a single *average* age composition and applied it to all the years represented in his data. This was fairly accurate for a long-lived fish during the period of rather stable fishing that he was mainly concerned with. An attempt to apply the same procedure to the Caspian vobla was made in 1928 by Borishchev (Chugunov 1935), but the result was less satisfactory. For fish with rather short life histories, variable recruitment, or variable fishing effort, it is desirable to determine the age composition for each year separately. This was first done by Boiko (1934) for the Azov zanders. Monastyrsky (1935) and Chugunov (1935) independently made the same kind of computation for the Caspian vobla. Both Boiko and Monastyrsky have later papers in which the method is applied to longer series of data.

Outside of the USSR, the biostatistical method was apparently first used in Canada by Bajkov (1933), in Derzhavin's form. Fry (1949) used yearly age samples to make a biostatistical assessment of a sport fishery for lake trout in Lake Opeongo. Fry's name for the utilized stock, or minimum estimate of stock size, was "virtual population," and outside of the USSR Derzhavin's method is often referred to as the "virtual population method." Fraser (1955) showed how a marking experiment can be advantageously combined with a biostatistical computation. Ricker (1958) examined some of the potential sources of error in the method, and identified the correct interpretation of the biostatistical rate of exploitation. Bishop (1959) examined the bias in estimates of mortality rates obtained from the regression of the logarithm of virtual population upon fishing effort.

Like other methods of population analysis, Derzhavin's biostatistical method has its strong and weak points. Whatever method is being used, the main thing is to know what exactly is being measured by the statistics that are computed. One way to determine this is to construct numerical models with known mortality rates, and then see what exactly a biostatistical computation will produce in the absence of sampling error. Effects of sampling variability on the estimates obtained can then be worked out from well-known statistical relations.

Sudden recruitment — The simplest kind of situation for a biostatistical study is as follows: (1) all the individuals of a year-class become vulnerable to fishing at the start of the same year of life; (2) there is no age-specific change in the instantaneous rate of fishing, F, or in the instantaneous rate of natural mortality, M, and hence also in the total mortality, $Z = F + M$; and (3) there is no increase or decrease in rate of fishing during the years represented by fish in the catch samples.

Table 1 shows an equilibrium situation of this kind. In line 6, the decrease of an initial 1000 fish

TABLE 1. Example of a biostatistical computation for equilibrium conditions, with rate of fishing the same at all ages. $S = 1 - A = e^{-z}$.

Statistic	Symbol	Age										
		3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	Total
1. Instantaneous rate of fishing	F	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
2. Instantaneous rate of natural mortality	M	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
3. Instantaneous total mortality rate	Z	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
4. Survival rate	S	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45
5. Mortality rate	A	0.55	0.55	0.55	0.55	0.55	0.55	0.55	0.55	0.55	0.55	0.55
6. Population at start of the year	N	1000	449	202	91	41	18	8	4	2	1	1816
7. Total deaths during the year	D	551	247	111	50	23	10	4	2	1	1	1000
8. Catch	C	413	185	83	37	17	8	3	2	1	1	750
9. Utilized stock (virtual population) at start of the year	V	750	337	152	69	32	15	7	4	2	1	1369
10. Biostatistical rate of exploitation	C/V	0.55	0.55	0.55	0.54	0.53	0.53	0.4	0.5	0.5	1.0	0.55
11. True rate of exploitation	u=C/N	0.41	0.41	0.41	0.41	0.41	0.44	0.4	0.5	0.5	1.0	0.41

is followed throughout their life by multiplying each year's stock by the survival rate, S. Total deaths, D, are found by subtraction (line 7), and the catch, C, is equal to FD/Z (line 8). The utilized stock, V, of each age is found by adding the catches cumulatively from the right (line 9).

For example, the utilized stock of age 9+ is $3 + 2 + 1 + 1 = 7$ fish, as shown in line 9 under age 9+; at age 8+ the utilized stock is $8 + 3 + 2 + 1 + 1 = 15$ fish, etc. This process is continued for all ages, the utilized stock of age 3+ being the sum of the catches of all ages, 750. The total utilized stock is then found by adding the individual utilized stocks of all the ages: that is, the figures in line 9 are added together to get the total, 1369, shown in the last column. (Notice that the complete computation from a single series of catches is possible only because Table 1 presupposes the same recruitment and the same mortality rates in all years.)

The ratio of the catch to the utilized stock, C/V, I have called the *biostatistical rate of exploitation.*

Apart from some irregularity due to small numbers at the older ages, C/V is equal to 0.55 at each age individually, and for the stock as a whole (line 10). Comparing it with C/N in line 11, it is 25% larger than the true rate of exploitation. In fact, C/V is exactly the same as the total mortality rate, A, shown in line 5. Under these simple equilibrium conditions, then, *the biostatistical rate of exploitation is an unbiased estimate of the total mortality rate in the population.* This result has been confirmed for other values of F and M, and it can easily be demonstrated algebraically.

A number of variations of the simple situation above can be examined. For example, what happens if natural mortality, M, increases with age? Numerical examples have shown that in this event the biostatistical rate of exploitation is a little *larger* than the total mortality rate (Ricker 1958 table 8.4). The amount of difference of course depends on how fast M increases, but for a fairly rapid increase in M (20% per year) the difference amounted to only about 5%.

Similarly, if natural mortality *decreases* with age, the biostatistical rate of exploitation becomes a little less than the total mortality rate.

Another common situation occurs where rate of fishing, F, increases or decreases with *time.* But as long as F remains the same at all ages during any given year, it is easy to show that this too produces only a small distortion (Table 2). Notice that the change in C/V applies to the years *before* the change in F takes place. If F increases, the value of C/V in earlier years becomes a little less than A, the change amounting to 6% at its largest (in the year immediately before the increase in F). In the first year with the new F value, C/V immediately increases to equal the new A and remains at that level.

Since a rather large increase in F has been used in Table 2, it appears that in most real situations there will be little distortion of C/V from this

TABLE 2. Comparison of biostatistical rate of exploitation, C/V, and total mortality rate, A, before and after a change from F = 0.6 to F = 1.2. The years –9 and +6 represent equilibrium conditions. Symbols are as in Table 1.[a]

Year	F	Z	S	A	N	C	V	C/V
–9	0.6	0.8	0.45	0.55	1816	750	1369	0.55
–8	0.6	0.8	0.45	0.55	1816	750	1368	0.55
–7	0.6	0.8	0.45	0.55	1816	750	1368	0.55
–6	0.6	0.8	0.45	0.55	1816	750	1368	0.55
–5	0.6	0.8	0.45	0.55	1816	750	1369	0.55
–4	0.6	0.8	0.45	0.55	1816	750	1373	0.55
–3	0.6	0.8	0.45	0.55	1816	750	1383	0.54
–2	0.6	0.8	0.45	0.55	1816	750	1404	0.53
–1	0.6	0.8	0.45	0.55	1816	750	1452	0.52
+1	1.2	1.4	0.25	0.75	1816	1171	1558	0.75
+2	1.2	1.4	0.25	0.75	1448	935	1242	0.75
+3	1.2	1.4	0.25	0.75	1358	877	1163	0.75
+4	1.2	1.4	0.25	0.75	1335	861	1142	0.75
+5	1.2	1.4	0.25	0.75	1330	857	1137	0.75
+6	1.2	1.4	0.25	0.75	1328	856	1136	0.75

[a]This table was prepared from a series of tables similar to rows 6–8 of Table 1. The fish of each year-class are followed throughout their lives, and their catches are summed to obtain the utilized stock of each age each year, and then the total for each year.

cause. An exception is where a fishery is being reestablished rapidly after a disruption caused by war or a legal closure. In such instances the effect of the sudden increase in F will be important.

All of the above presupposes that rate of fishing is the same at all ages in any given year. Actually it is seldom that all ages are equally vulnerable. However, *this condition can usually be met quite simply by limiting the biostatistical computation to the older age-groups*, i.e., those that are fully vulnerable or "fully recruited." If this were done,[2] the interpretation of C/V is unambiguous: it estimates the *total* mortality rate, A, for these ages during the year in question, with little or no systematic bias. The instantaneous mortality rate for fully vulnerable ages can then be estimated as $Z = -\log_e(1-A)$.

Protracted recruitment — In point of fact, biostatistical estimates have usually been made for the total of all the important ages in a catch, so we must consider the situation when rate of fishing increases with age. During the years of recruitment the younger age-groups in a stock are less vulnerable than the older ones. Typically, each year-class starts out with a small F, and over a period of years F increases until its maximum value is reached. The rate of fishing, F, and the rate of exploitation, C/N, are different for each age during the recruitment period. Designating individual year-classes present in a stock by the subscript i, we should compare C_i/V_i at each age with C_i/N_i and other known population parameters.

Table 3 gives an example based on a stock under equilibrium conditions (no change in mortality rates or in recruitment from year to year). The value of F is the same for all fish of age 6 and older, so for these ages C_i/V_i is equal to the total mortality rate A_i (= 0.59). At ages 3, 4, and 5, however, C_i/V_i is always less than A_i, though it is greater than the true rate of exploitation, C_i/N_i.

Consider now the figures for the stock as a whole, shown in the last column of Table 3 (these are the figures usually tabulated in biostatistical studies). The utilized stock, 1301, is only a little more than half of the true population of 2386. The biostatistical rate of exploitation, C/V, is 0.35, which is considerably less than the total mortality rate (0.42) and less than the true rate of exploitation of fully recruited fish (0.39). However, C/V is much larger than the overall rate of exploitation of the whole stock, which is only C/N = 0.19.

It is evident that when recruitment ages are included in the totals, neither C/V nor C/N are

[2]In his first paper on the zanders, Boiko (1934) excludes the future catches of the youngest age-group (age 3) from the total utilized stock, which goes a long way toward meeting this condition. However, the age-4 fish, also, were not fully vulnerable to the fishing in progress. In his 1964 paper, Boiko includes the age-3 year-class in the utilized stocks, but excludes those represented by fish of age 2 or age 1.

TABLE 3. Example of a biostatistical computation under equilibrium conditions, with ages 3+ to 5+ incompletely recruited. Symbols as in Table 1.

		Age										
		3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	Total
1	F	0.05	0.3	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.6	–
2	M	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	–
3	Z	0.35	0.6	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	–
4	S	0.70	0.55	0.45	0.41	0.41	0.41	0.41	0.41	0.41	0.41	–
5	A=D/N	0.30	0.45	0.55	0.59	0.59	0.59	0.59	0.59	0.59	0.59	0.42
6	N	1000	705	387	174	71	29	12	5	2	1	2386
7	D	295	318	213	103	42	17	7	3	1	1	1000
8	C	42	159	133	69	28	11	5	2	1	0	450
9	V	450	408	249	116	47	19	8	3	1	0	1301
10	C/V	0.09	0.39	0.53	0.59	0.60	0.58	0.6	0.7	1.0	–	0.35
11	C/N	0.04	0.23	0.34	0.40	0.39	0.38	0.4	0.4	1.0	–	0.19

very meaningful statistics. In this example the true mean rate of exploitation, 19%, looks like a very moderate fraction of the total stock. Yet the larger and more valuable fish are dying at the rate of nearly 60% per year, of which the fishery takes two-thirds. The value of C/V, 35%, comes closer to the true 39% rate of capture *of large fish*, though it is still too low. But even this degree of agreement is fortuitous, and does not necessarily appear with other combinations of F and M.

We must conclude that the biostatistical rate of exploitation for a whole stock has no exact interpretation in terms of population parameters. It can of course be used as an arbitrary index of effectiveness of fishing, especially if a more detailed analysis is not possible. That is, we may compare C/V for 1 year with that for earlier or later years to show whether fishing rate is increasing, or decreasing, or staying steady. However, even for this purpose, C/V should be modified by eliminating any scarce young age-group that contributes little to the catch in numbers, and still less in weight. Above all, *the minimum age included in a biostatistical computation should be the same in all years.*

Estimation of year-class strength — A very useful feature of Derzhavin's biostatistical method is that it can provide an estimate of the relative size or "strength" of successive individual year-classes in a stock. This estimate is the "utilized year-class strength" of Voevodin, ΣC_i, found by adding the catch of the appropriate age for all the years that the year-class is present in the fishery. These figures can be compared with environmental factors to discover relations and make predictions.

There is also available the total utilized stock present each year, V. Hence, with data for a long period of years, it becomes possible to compare the size of parental stocks with the number of commercial-sized progeny that they produce, to see what kind of relation exists. For this purpose the parental utilized stock can be estimated in different ways: as numbers of fish, their total weight, the number or weight of *mature* individuals, the potential egg production, and so on.

In the simple situation where F and M do not vary with time the size of the year-class produced in a given year is proportional to ΣC_i, and the stock present in a given year is proportional to V. Change in F with age makes no difference, provided it is the same in all years at any given age.

If the spawning period occurs just *after* the fishery each year, the "utilized carry-over" of adults (i.e., those that will be caught in future years) may be a better index than V of the intensity of the spawning just completed (this depends on the relative size of M and F). For a fully recruited year-class, the utilized carry-over is simply equal to the sum of its C_i values for all future years. At younger ages this statement does not apply, but often the recruitment ages consist mainly of immature fish, so can be omitted from a computation of *mature* stock.

Everything said so far in this section requires that rate of fishing be constant from year to year. Unfortunately, when F changes with time everything becomes more complex. Consider Table 2, for example. When F increases, both the catch, C, and the utilized stock, V, increase immediately. Subsequently both C and V decrease again, but whereas C levels off at a value greater than the original, V declines to a level less than the original. More generally, the final level of V may be either less or greater than the original, depending on the absolute values of F and M. And although the

number of fish in the catch has increased, their average age is less than formerly, so their total *weight* may be either greater or less.

During the years of recruitment there are even greater difficulties. However, the difficulties can often be overcome by patient analysis. If F increases, so will the total mortality rate, Z, at all ages, and this increase can be estimated from the value of A_i ($=C_i/V_i$) computed from the fully recruited ages. Hence, models can be constructed, using plausible estimates of M, and from them it is possible to compute approximate adjustments for the values of V_i that are consistent with the observed age distributions. Usually these adjustments will not be too large, and even the unadjusted estimates may be quite informative, as Boiko (1964) has shown.

Natural mortality — Since the biostatistical rate of exploitation is in fact an estimate of the *total* mortality rate (for fully recruited fish), it follows that the data do not provide any direct estimate of the true rate of exploitation and hence the rate of natural mortality. This is in fact the principal inadequacy of Derzhavin's method.

If natural mortality is really absent, then of course total mortality rate and rate of exploitation are the same thing. Some authors have stated, or implied, that natural mortality is negligible among the important commercial ages in the stocks they were studying. Thus, they would regard our Table 3 as unrealistic, for it uses a moderately large natural mortality rate (M = 0.3). However, for populations where actual estimates of natural mortality have been made, it invariably turns out to be quite appreciable. The value of M usually lies between 0.2 and 0.5 for the middle range of ages in stocks where the maximum known age is 15–25 years.

Other authors have recognized the probable existence of considerable natural mortality but, having no quantitative estimate of it, it tends to be forgotten as the analysis proceeds. In particular, the biostatistical rate of exploitation has usually been treated as though it were the true rate of exploitation, even in situations where this will make for rather serious misinterpretation.

Obviously an effort should be made to estimate true rate of exploitation, and hence natural mortality rate, using whatever method is most suitable: for example, data on fishing effort, marking or tagging, and so on (see Ricker 1958, and Zasosov 1969). If this is not possible, then trial computations can be made using two or three possible natural mortality rates, to get an idea of how they would affect the analysis.

Variation in recruitment — When F is the same at all ages, the estimated value of C/V is not changed if recruitment varies from year to year. This fact has been confirmed by calculation, and indeed it is clear enough with the unaided imagination. Thus, an advantage that the biostatistical method has over certain other methods is that *for fully recruited fish, C/V is an unbiased estimate of total mortality rate regardless of fluctuations in recruitment from year to year.* This, of course, is subject to minor qualifications if M varies with age, or if F varies with time, as described earlier.

When the recruitment ages are included in a biostatistical computation, variation in year-class size produces some fluctuation in the C/V estimates for total stock. The amount of bias depends on the values of F and M at successive recruitment ages, and on the amount of change in year-class "strength," so no general assessment of its importance seems possible. However, for each individual instance this effect can be estimated approximately, and adjustments can be made if it seems worthwhile.

Incorrect age classification — It is quite common for determinations of age to be revised in the light of later experience. Sometimes this happens because an improved method of age determination has been introduced: for example, using otoliths or fin rays instead of scales. Other times objective information from fish of known age will modify the interpretation of materials already in use. In either event, the commonest change is in the direction of *increasing* the estimated ages.

What is the effect of incorrect age determination on estimates of the utilized population? We may observe that no fish are lost because they are given the wrong age. They all appear in the biostatistical data at one age or another. Hence, it might be argued that the estimates of utilized populations should not be affected, since they are obtained by summing the catches. Unfortunately, this argument is fallacious. The older a fish is when caught, the oftener he gets counted in the biostatistical computation; that is, the more utilized stocks he will appear in. Hence, when age determinations are too low, the utilized stocks also are too small, and the biostatistical rates of exploitation, C_i/V_i, are too large.

Thus, *age determination without consistent bias is an important prerequisite for Derzhavin's method,* and of course for other methods as well.

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Ambicoloration in a Petrale Sole (*Eopsetta jordani*)

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FORRESTER, C. R., AND M. S. SMITH. 1971. Ambicoloration in a petrale sole (*Eopsetta jordani*). J. Fish. Res. Bd. Canada 28: 1672–1674.

Ambicoloration, which was complete except for a small unpigmented area on the blind side of the head and a portion of the pectoral fin, was noted in a petrale sole (*Eopsetta jordani*) taken off the west coast of Vancouver Island, B.C. The specimen also showed anomalous development of the dorsal fin and had two fused vertebrae near the caudal peduncle.

FORRESTER, C. R., AND M. S. SMITH. 1971. Ambicoloration in a petrale sole (*Eopsetta jordani*). J. Fish. Res. Bd. Canada 28: 1672–1674.

Les auteurs rapportent un cas d'ambicoloration d'une plie anglaise (*Eopsetta jordani*) capturée au large de la côte occidentale de l'île de Vancouver, Colombie britannique. L'ambicoloration était totale, à l'exception d'une minime partie du côté aveugle de la tête et d'une portion de la nageoire pectorale. De plus, la nageoire pectorale était irrégulière et deux vertèbres voisines du pédoncule caudal étaient fusionnées.

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DURING June 1970, an unusually pigmented petrale sole (*Eopsetta jordani*) was taken in a trawlnet from grounds off the west coast of Vancouver Island, B.C. The specimen, a female, was recovered by Mrs S. Barclay on the fillet line at Dennis' Shellfish Company Limited in Victoria, B.C. On the usually unpigmented blind side, ambicoloration (replication of typical eyed-side markings) was complete except for a small area on the head and a portion of the pectoral fin (Fig. 1). Abnormal coloration in

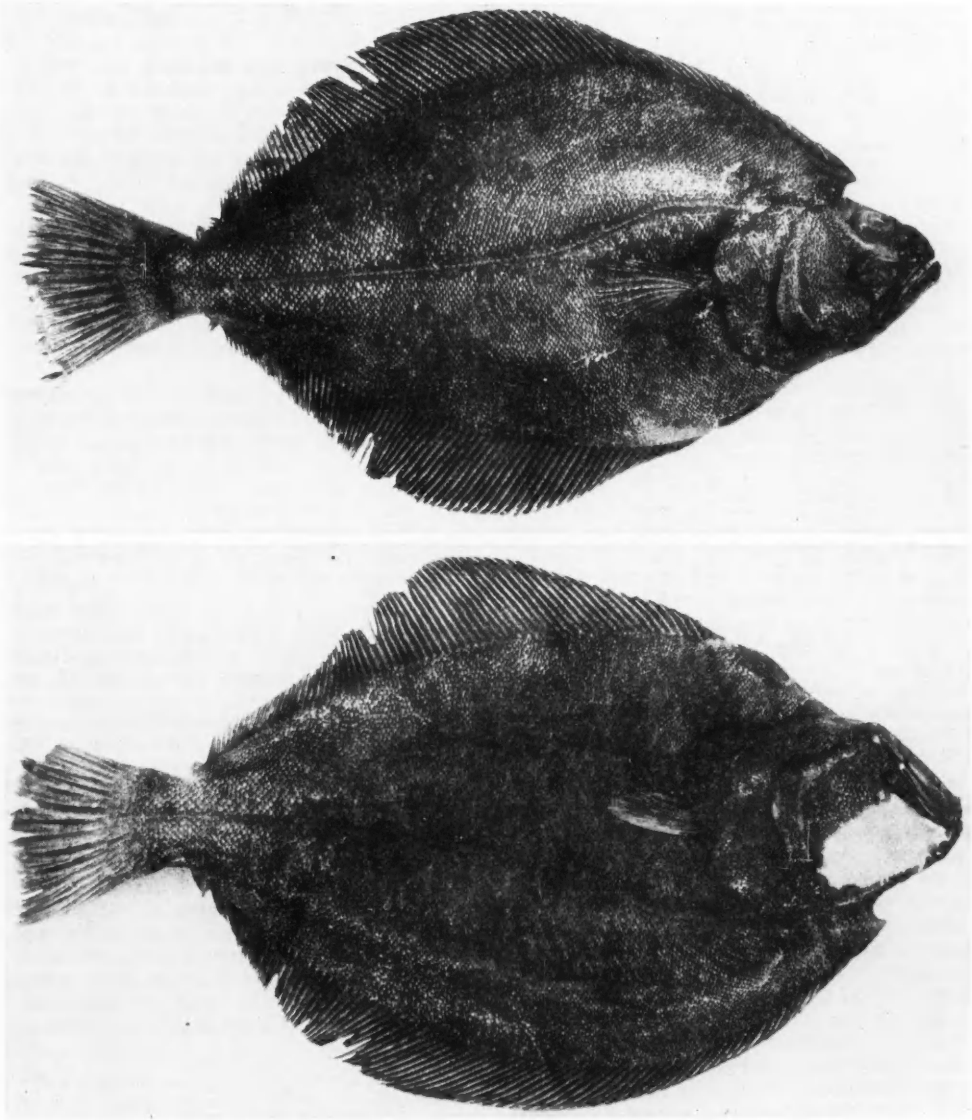

FIG. 1. Eyed and blind sides of an ambicolored petrale sole, 404 mm standard length, taken off the west coast of Vancouver Island. (Photograph by C. J. Morley.)

flatfish is not rare (Dawson 1962), but is uncommon enough to arouse considerable interest. Although ambicoloration has been reported in the genus *Eopsetta* (from southern Japan Sea — Imaoka 1959; Imaoka and Nishimura 1964), it apparently has not been previously recorded for this particular species.

In addition to ambicoloration, the petrale sole showed anomalous development of a fleshy hook at the anterior end of the dorsal fin and incomplete migration of the left eye. The occurrence of these anomalies, in association with the extensive ambicoloration, agrees with expectations according to the "rule" of Gudger and Firth (1935), which, as stated by Dawson (1962) is: "whenever the entire lower surface is colored like the upper or when about 1/4 to 1/3 of the head surface of the blind side is colored, the rotating eye will not completely migrate past the dorsal crest and the anterior dorsal fin will be hooked." In two ambicolored specimens of *Eopsetta* reported from the Japan Sea, the one that possessed the hooked dorsal fin and incomplete eye migration displayed more ambicoloration than the other specimen (Imaoka and Nishimura 1964 fig. 2, 3).

TABLE 1. Measurements and counts on two petrale sole.

	Ambicolored	Normal
Measurements[a]		
Standard length	404	398
Total length (to centre of caudal)	119.1	118.1
Head length	30.4	28.9
Fleshy orbit — dorsal, ventral	4.7–4.7	5.0–5.5
Interorbital width	2.2	1.8
Snout length — to lower eye	5.7	5.3
Maxillary length	9.2	8.3
Body width (greatest)	49.8	48.7
Caudal peduncle width	9.7	9.0
Pectoral fin length (eyed side)	15.1	15.6
Pelvic fin length (eyed side)	7.4	7.0
Snout to dorsal origin	12.9	7.5
Snout to anal origin	33.4	33.4
Snout to pelvic origin	28.5	23.1
Snout to pectoral origin	28.5	27.6
Counts		
Dorsal rays	95	96
Anal rays	75	75
Pectoral rays (eyed side)	13	13
Pelvic rays (eyed side)	6	6
Gill rakers	5+16	5+14

[a]Standard length in millimeters; other measurements given as percentages of standard length.

The only other abnormality in the petrale sole, found in a radiograph of the specimen, was fusion of the two vertebra immediately preceding the penultimate vertebra. Counts and measurements were made on the ambicolored fish for comparison with those from a "normal" female specimen (Table 1).

The specimen has been deposited in the museum of the Institute of Animal Resource Ecology at the University of British Columbia (Cat. no. B.C. 70-6).

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Sterols of a Brachiopod, *Terebratalia transversa*

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IDLER, D. R., AND P. WISEMAN. 1971. Sterols of a brachiopod, *Terebratalia transversa*. J. Fish. Res. Bd. Canada 28: 1675–1676.

The sterol composition of a brachiopod is remarkably similar to that of a pelecypod. The principal sterols of both are cholesterol, brassicasterol, and 24-methylenecholesterol, and even the relative proportions are nearly identical. These invertebrate groups were classed together before this century, but have since been shown to be structurally unrelated.

IDLER, D. R., AND P. WISEMAN. 1971. Sterols of a brachiopod, *Terebratalia transversa*. J. Fish. Res. Bd. Canada 28: 1675–1676.

La teneur en stérol d'un brachiopode est remarquablement semblable à celle d'un pélécypode. Les principaux stérols dans les deux organismes sont le cholestérol, le brassicastérol et le 24-méthylènecholestérol. Les proportions sont même identiques dans les deux. Au siècle dernier on avait classé ces deux groupes ensemble, mais par la suite leurs structures se sont avérées sans rapport.

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BRACHIOPODS (lamp shells) are of great interest phylogenetically as they are one of the most ancient groups of animals. They have inhabited the sea bottom since Cambrian time, and during their most flourishing periods, Ordovician and Silurian, they numbered approximately 2000 species. Their shells are widely distributed and abundant in rock strata of marine origin and are useful in correlating such deposits. Brachiopods have descended relatively unchanged through the Paleozoic and Mesozoic eras, although their numbers have declined, until today there are approximately 70 living genera and 225 species. One species, *Lingula*, is possibly the oldest living genus of animal and it is much as it was in the Ordovician period, 400 million years ago.

All brachiopods are marine, solitary, and usually attached to rocks on the sea bottom by a projecting muscular stalk, the peduncle. Most species are found in shallow water but a few go deeper, even to 18,000 ft. Brachiopods were originally classified under Mollusca, as their bivalve calcareous shells bear a superficial resemblance to that group. However, in brachiopods the two valves enclose the body dorsally and ventrally instead of laterally, and the ventral valve is typically larger than the dorsal. The animal contained within the shell strongly resembles the fundamental Bryozoan plan, and three related phyla, Brachiopoda, Bryozoa, and Phoronidae, are referred to as the "lophophorates." All members have a food-catching organ, a lophophore; this is a circular or horseshoe-shaped fold of the body wall that encircles the mouth and bears numerous ciliated tentacles. The Brachiopoda are divided into two classes, based primarily on the articulation of the two valves. In the Articulata (e.g., *Terebratalia*), the valves are hinged by interlocking processes that greatly restrict the degree of gape. In the Inarticulata (e.g., *Lingula*), the shells are held together by muscles and thus have greater flexibility.

There is no published information on the sterols of brachiopods, and the purpose of this investigation was to fill the void in the comparative biochemistry of bivalves.

The sterols of one brachiopod, *Terebratalia transversa* (Sowerby), were examined by gas–liquid chromatography (GLC). This species, called the red lamp shell, is the most common brachiopod on the west coast, covering an area from Alaska to southern California, from the low-water mark to 100 fath. Although brachiopods are not related to molluscs, the sterol composition of *Terebratalia* is surprisingly similar to the sterols of pelecypods (Idler and Wiseman 1971a) as Table 1 demonstrates. It is not a purpose of this note to provide rigorous proof of the structures of the brachiopod sterols. Such proof has been well documented for mollusc and other invertebrate sterols in a series of papers from this laboratory, as has the adequacy of the GLC system for resolution of closely related sterols present in the complex mixtures. Sterols of the

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TABLE 1. Gas–liquid chromatographic separation of sterols in a pelecypod, the scallop *Placopecten magellanicus*, and in a brachiopod, the red lamp shell *Terebratalia transversa*, as methyl ether derivatives on a mixed column (4 mm × 14 ft) of 3% XE-60 and 3% NGS (1:1). Retention times of sterols were calculated relative to cholestane added before GLC.

Sterol no.	Name	% composition	
		Pelecypod	Brachiopod
1	22-*cis*-24-norcholesta-5,22-dien-3β-ol(?)	–	0.6
2	22-*trans*-24-norcholesta-5,22-dien-3β-ol	6.3	3.8
3	22-*cis*-cholesta-5,22-dien-3β-ol	3.7	0.6
4	22-*trans*-cholesta-5,22-dien-3β-ol	10.9	4.6
5	Cholesterol	31.8	32.2
6	Brassicasterol	17.7	16.7
7	7-Dehydrocholesterol	–	0.6
8	22:23-Dihydrobrassicasterol or campesterol	3.0	3.9
9	24-Methylenecholesterol	17.4	20.4
10	β-Sitosterol	5.4	–
11	Fucosterol	0.4	2.8
12	28-Isofucosterol	2.7	3.3
13	$C_{30}H_{50}O$ sterol (29-Methylisofucosterol)	0.7	–
	Unidentified components	–	10.5(4)

pelecypod, *Placopecten magellanicus* (Gmelin), the sea scallop, have been rigorously identified by GLC and mass spectrometry after separation by preparative GLC (Idler and Wiseman 1971b). Eleven sterols are present in scallop sterol mixture and 15 in the brachiopod; the three principal sterols, cholesterol, brassicasterol, and 24-methylenecholesterol, represent approximately the same percentage of the total sterol of scallop and brachiopod.

The function of such a diversity of complex sterols in brachiopods and molluscs, whether structural or metabolic or both, is unknown, but the similarity in composition suggests that these sterols perform similar and perhaps specific functions. It is unfortunate that no data are available on Bryozoan sterols. It would be interesting to see if they resemble brachiopod and pelecypod sterols. Certain classes of invertebrates are characterized and thus related by having unique sterol compositions, and pelecypods have shown a greater diversity in sterol composition than other molluscs, e.g., gastropods, cephalopods, and Amphineura (chitons). Gastropods contain sterol mixtures but trend towards a larger percentage of cholesterol. Cephalopods contain primarily cholesterol and the Amphineura, Δ^7-cholesterol.

The origin of brachiopod and mollusc sterols is of interest. Both groups feed on organic particles and microorganisms (diatoms, protozoans, etc.) suspended in the water. Sterols of the oyster, *Crassostrea virginica* (which are very similar to scallop sterols), are partly of exogenous origin (Tamura et al. 1964). Sterol biosynthesis was also demonstrated in this species, and muscles and clams are capable of synthesizing mono-unsaturated Δ^5-sterols from acetate-2-C^{14} (Fagerlund and Idler 1960). A transformation of injected cholesterol-4-C^{14} into radioactive 24-methylenecholesterol in vivo has been demonstrated in the clam (Fagerlund and Idler 1961). It is probable that brachiopods contain the same enzyme systems as molluscs for conversion of one sterol to another.

Our results have demonstrated a similarity in sterol composition between two invertebrate groups, brachiopods and pelecypods, which were classified together before this century, but have since been shown to be structurally unrelated.

Acknowledgments — This manuscript is dedicated to Dr C. Berkeley who has contributed so much to our knowledge of marine invertebrates. We thank Dr W. E. Ricker, who collected the brachiopods used in this study.

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Pachycerianthus (Ceriantharia) from British Columbia and Washington

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ARAI, M. N. 1971. *Pachycerianthus* (Ceriantharia) from British Columbia and Washington. J. Fish. Res. Bd. Canada 28: 1677–1680.

Pachycerianthus fimbriatus specimens from seven collecting areas are described. Many of these specimens closely resemble *Pachycerianthus torreyi* Arai 1965 from California, but the range of variation is wider. *Pachycerianthus torreyi* and *Pachycerianthus plicatus* are considered junior synonyms of *P. fimbriatus*.

ARAI, M. N. 1971. *Pachycerianthus* (Ceriantharia) from British Columbia and Washington. J. Fish. Res. Bd. Canada 28: 1677–1680.

L'auteur décrit les spécimens de *Pachycerianthus fimbriatus* de sept zones d'échantillonnage. Plusieurs ressemblent à *Pachycerianthus torreyi* Arai 1965 de Californie, mais la gamme des variations en est plus étendue. On relègue *P. torreyi* et *Pachycerianthus plicatus* au rang de synonymes juniors de *P. fimbriatus*.

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ALTHOUGH Ceriantharia are commonly found by divers and in dredge hauls in British Columbia waters, no previous work has been done on them. The specimens described here were collected from seven areas of the province and northern Washington state. A glossary of the terms applicable to the Ceriantharia in these descriptions is included in Arai (1965).

Many of these specimens closely resemble *Pachycerianthus torreyi* (Arai 1965) from California, but the range of variation is wider. It is concluded that *P. torreyi* is a junior synonym of *Pachycerianthus fimbriatus* (McMurrich 1910) and that all the animals in the present study also belong to this species.

Materials and Methods

Descriptions are based on animals collected from the following localities between 1961 and 1970; 10 specimens from Henry Bay, north shore, i.e., north end of Denman Island, inner side of bar running out to Seal Islets; 2 specimens from Saanich Inlet, Finlayson Arm, off point on north side of Misery Bay; 12 specimens from Fatty Basin, Barkley Sound; 10 specimens from Howe Sound, Queen Charlotte Channel, off Whytecliff Park, West Vancouver; 10 specimens from Departure Bay, near Brandon Island; 2 specimens from Clear Passage, east end of passage, off NE corner of Cosine Island, i.e., off NE side of Principe Channel; 2 specimens from Case Inlet, Puget Sound. The Henry Bay specimens and 10 of the Fatty Basin specimens were intertidal or in shallow water from sand, gravel, or shell bottoms. The Case Inlet specimens were obtained by grab at 55 m depth. The remaining specimens were dug by divers at 6–18-m depths from mixed mud, sand, and rock bottoms.

Fatty Basin shallow water and Henry Bay animals were anaesthetized in equal parts of sea water and a solution of 0.36 M $MgCl_2 \cdot 6H_2O$. They were fixed briefly in 10% neutral formalin (with excess of $MgCO_3$), overnight in picro–formol solution (1 part concentrated formalin, 3 parts saturated picric acid), and stored in 70% ethanol. In each instance, the solutions were pipetted into the coelenteron. Saanich Inlet specimens were treated as above, except that they were postfixed in Bouins instead of picro–formol. Departure Bay, Fatty Basin deep water, and Howe Sound specimens were anaesthetized, fixed in neutral formalin overnight, and stored directly in ethanol. Clear Passage and Case Inlet specimens were fixed in formalin and transferred several days later to ethanol. Although degree of contraction varied widely with preservation method, all animals examined were at least 5 cm long following fixation. All contained sexual products, having been collected in the summer (June 3 to November 18).

General morphology — All specimens examined belonged to the family Cerianthidae i.e., lacked acontiods or cnidorages. They were all found to belong to the genus *Pachycerianthus* Roule 1904.

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This genus includes Cerianthidae with the second couple of protomesenteries short and sterile, and the arrangement of metamesenteries in each quartette M, B, *m*, *b* more or less distinct. However, two of the Henry Bay animals show a reversal of the usual metamesenterial pattern (in a quartette other than the first) to *m*-M- on one side only, and a third shows the reversal on both sides. Carlgren (1924) found similar breaks in the pattern in *Pachycerianthus plicatus*.

Arai (1965) described the species *P. torreyi* from southern California. All 48 northern animals were examined for characteristics that had proved stable and useful for diagnosis in the 1965 study. In many specimens craspedonemes are absent or sparse on the upper half of the M_1 mesenteries. Other than this very minor point, 27 specimens, including at least half the animals from each collecting site, agree with the following diagnosis of *P. torreyi*: siphonoglyph running length of actinopharynx; directive mesenteries extending well beyond siphonoglyph; second protomesenteries between one and two times the length of directives; M_1 definitely longer than any other mesentery; M_2 longer than M_2; m_2 and m_3 shorter than m_1; B_1 shorter than P_3; M_1 with trineme almost to end of mesentery, craspedonemes scattered over most of its length, very short or no mononeme.

The remaining specimens differ from the diagnosis. Eight animals (four Fatty Basin, one Howe Sound, one Case Inlet, two Departure Bay) have P_2 mesenteries longer than 2× the P_1, although less than 2.5×. In addition, one Henry Bay specimen on one side only contains a directive mesentery continued as an unusually broad flat ribbon longer than the second protomesentery. In one Henry Bay specimen, although the expected relative lengths of the macromesenteries are maintained, three couples of M mesenteries reach within $\frac{1}{10}$ of the column from the aboral pore; in one Fatty Basin specimen, M_2 on one side only approaches the length of the M_1; and in two Howe Sound specimens, the M_3 couple is almost as long as the M_1. For these four animals it is debatable whether the M_1 may be considered "definitely longer than any other mesentery." In 13 animals (six Henry Bay, one Fatty Basin, two Howe Sound, one Case Inlet, and three Departure Bay) the M_2 is longer than the M_3 on one or both sides (10 on one side, three on both).

In view of the variation in the above characters, further structures were checked for stability in 10 specimens from Departure Bay. These animals agreed with *P. torreyi* specimens from California in the following points: directive labial tentacle present; hyposulcus less than $\frac{1}{10}$ length of siphonoglyph; hemisulci distinct, flat orally, continued down directive mesenteries as filaments; third protomesenteries short, sterile, with a highly convoluted mononeme, longer than P_1; reproductive organs in macrosepta only. (With reference to the P_3, however, one of the Henry Bay specimens had a third protomesentery on one side only that contained reproductive organs and was longer than the first and second protomesenteries.) The Departure Bay specimens had 8–10 mesenteries attached to the siphonoglyph, the California specimens 10–12.

Coloration of live animals — Column red-brown, darkest just below oral disc and toward aboral pore, with narrow buff ring immediately around aboral pore, in some specimens with purple or green tinge to upper portions. Marginal tentacles various shades between reddish fawn and dark purple, unbanded or with irregular patches of darker brown and small opaque lighter spots giving an overall impression of banding on the inner sides, in some specimens with a narrow light band on the inner side of the base. Labial tentacles fawn, in some specimens shading to pink or light purple at the tip, in some specimens darker on inner sides to give a longitudinally lined appearance. Oral disc dark red, or purplish brown, or with inner lighter ring up to four-fifths the width of the disc showing still lighter radial markings.

The above description is based on 44 animals, no color notes having been made on the Clear Passage or Case Inlet specimens. No correlations between particular color patterns and variations in internal anatomy were noted. Figure 1 shows the variation in pattern found in a small group of *Pachycerianthus* in Departure Bay. As with the internal morphology, the British Columbia specimens may agree with the description of *P. torreyi* from southern California but show a wider range of variation.

Nematocysts — The following data are based on fresh squashes of three animals from Fatty Basin: of column, atrichs 35.6–79.2 × 11.6–35.2 μ numerous, microbasic *b*-mastigophores 16.0–41.6 × 4.8–10.4 μ common, holotrichs 45.2–68.0 × 16.0–22.4 μ fairly common; of marginal tentacles, atrich single one seen, microbasic *b*-mastigophores 13.6–52.4 × 3.2–12.2 μ common, spirocysts 22.4–44.4 × 2.4–7.6 μ common; of labial tentacles, atrichs single one seen, microbasic *b*-mastigophores 19.2–40.0 × 3.2–11.2 μ common, spirocysts 16.4–29.6 × 2.4–6.4 μ numerous; of actinopharynx, atrichs 35.6–40.0 × 5.6–16.4 μ common, microbasic *b*-mastigophores 17.2–40.4 × 3.6–10.0 μ common, spirocysts seen in one speci-

FIG. 1. *Pachycerianthus fimbriatus* specimens in Departure Bay showing the variation in color pattern. (Courtesy of Mr P. Fraser.)

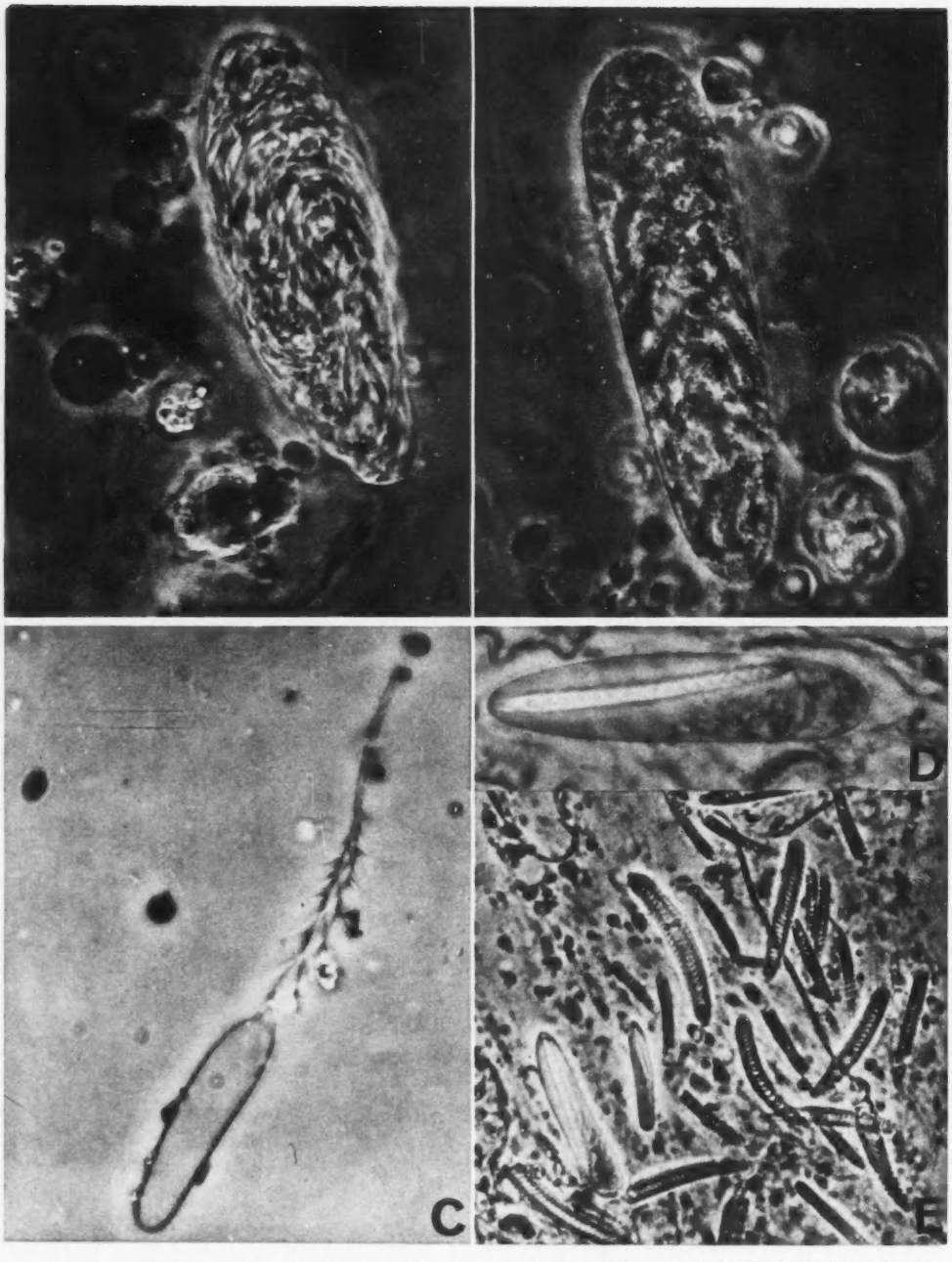

FIG. 2. Nematocyst types: A, atrich of column; B, holotrich of column; C, evaginated microbasic *b*-mastigophore of marginal tentacle; D, unevaginated microbasic *b*-mastigophore of marginal tentacle; E, spirocysts and microbasic *b*-mastigophore of marginal tentacle. A to D, 840×; E, 375×.

men only, holotrichs seen in one specimen only; of trineme of macrospetum, atrichs 25.6–29.6 × 5.2–9.2 μ rare, microbasic *b*-mastigophores 32.0–48.4 × 6.0–14.4 μ common, spirocysts numerous; of peloton of microseptum, microbasic *b*-mastigophores 14.8–44.8 × 4.0–10.8 μ numerous, spirocysts 16.8–23.2 × 3.6–5.2 μ rare; of tube, atrichs 25.2–72.4 × 6.8–33.2 μ common, microbasic *b*-mastigophores 11.2–41.2 × 2.4–12.0 μ rare, holotrich single one seen, spirocysts 26.4–31.2 × 2.8–4.0 μ rare.

The same nematocyst types were seen in squashes of corresponding portions of a single animal from Departure Bay. Measurements were not made, however. Examples of each of the types of nematocysts are shown in Fig. 2. This cnidom agrees with that for the California specimens of *P. torreyi.*

Discussion — Developmental anomalies are not unusual in coelenterates. Striking, rare variations, particularly if the animal is not bilaterally symmetrical, are usually assumed to be such anomalies. In the present study, such characters include the single unusually long directive mesentery found in one Henry Bay specimen, and the single unusually long and fertile third protomesentery found in another Henry Bay specimen. Aside from these characters, however, the northern population shows a wider range of variation than those examined from California, particularly with respect to the relative lengths of the P_2 and P_1, the relative lengths of the M_2 and M_3, and the relative lengths of the M_1 and other macrosepta.

It is not clear why the range of variation should be greater in northern waters. A wider variety of habitats was sampled, but no correlation between habitat and morphology was found, the range being great in any one collecting area.

In the previous study (Arai 1965) *P. torreyi* was considered most similar to *P. fimbriatus* McMurrich 1910 and *P. plicatus* Carlgren 1924, differing only in the relative lengths of the M_2 and M_3 mesenteries. As noted above, this is variable in the British Columbia specimens. McMurrich (1910) described *P. fimbriatus* primarily from two specimens from Gisser Island, Indonesia. It has not been possible to locate the original specimens, but the description and diagram are reasonably detailed. Carlgren (1924) described *P. plicatus* from two specimens from Banda Island, Indonesia. He differentiated this species from *P. fimbriatus* mainly on the presence or absence (the latter in *P. plicatus*) of a mononeme on the M mesenteries. As shown in Arai (1965) a mononeme may be present or absent on the M_1 in *P. torreyi.* In addition, Carlgren (1924) mentioned the distribution of craspedonemes, which is also highly variable. *Pachycerianthus plicatus* and *P. torreyi* should therefore be considered junior synonyms of *P. fimbriatus.*

All studies on *P. fimbriatus* agree on the following characters: directive labial tentacle present; 8–12 mesenteries attached siphonoglyph; directive mesenteries extend well beyond siphonoglyph; second protomesenteries between 1 and 2.5× length of directives; in most specimens M_1 definitely longer than any other mesentery; reproductive organs in macrosepta only; m_2 and m_3 shorter than m_1; B_1 shorter than P_3. Carlgren (1924), Arai (1965), and the present study also agree on the following characters that were not noted by McMurrich (1910): siphonoglyph runs length of actinopharynx; hyposulcus short; hemisulci distinct, continued down directive mesenteries as filaments; M_1 with trineme almost to the end of mesentery, very short or no mononeme.

The clarity with which *P. fimbriatus* can be distinguished from other species included in the genus depends, in good part, on the detail in which they have been described. Most species have been based on a very small number of specimens, little data being given. *Pachycerianthus benedeni,* Roule 1904, the type species of the genus, was very vaguely described from a single specimen from the Inland Sea of Japan. Roule (1904b) stated, however, that the mesenteries show a biseptal arrangement rather than the quatroseptal disposition found in *P fimbriatus.*

Pachycerianthus insignis Carlgren 1951 was also based on a single incomplete specimen from the Gulf of California. Several M and *m* mesenteries reach down almost to the proximal end of the body. *Pachycerianthus dohrni* (van Beneden 1923) from the Mediterranean has at least four couples of mesenteries reaching near to the aboral pore of adult specimens (see also the description by Torelli (1938) of the mesenteries of *Cerianthus viridis,* stated by Carlgren (1940) to be a synonym of *P. dohrni*). *Pachycerianthus multipicatus* Carlgren 1912 from northern Europe has a siphonoglyph with six mesenteries attached. All the M mesenteries are very long except the couple closest to the multipication chamber. In most specimens of *P. fimbriatus* the M_1 are definitely longer than any other mesenteries and in all specimens definitely longer than the *m* mesenteries. In the specimens examined to date a maximum of three couples reach near to the aboral pore.

Pachycerianthus johnsoni (Torrey and Kleeberger 1909), described from two specimens from southern California, differs from *P. fimbriatus* in that the directive mesenteries do not extend beyond the

siphonoglyph and the diagram shows the B_1 to be longer than the P_3. Gonads are frequently borne on the third order mesenteries. In *Pachycerianthus monostichus* McMurrich 1910 from Indonesia, the directive mesenteries hardly project below the lower border of the siphonoglyph and as a result, the diagram shows the P_3 at least seven times the length of the P_1. The diagram also shows the B_1 longer than the P_3. *Pachycerianthus aestuari* (Torrey and Kleeberger 1909) from southern California possesses a very broad siphonoglyph that does not reach the lips of the actinopharynx, and the mesenteries show a biseptal disposition.

Pachycerianthus maua (Carlgren 1900) from east Africa possesses an unusual type of aboral craspedoneme (see Carlgren 1912a, b). In *Pachycerianthus solitarius* (Rapp 1829) from the Mediterranean, craspedonemes of the trineme are absent, there being a single craspedoneme at the aboral end of each M mesentery. Torelli (1963) has placed the larval species *Pachycerianthus bicyclus* (Torelli 1961) in synonymy with *P. solitarius*. In summary, *P. fimbriatus* can presently be distinguished by at least one stable character from any other species in the genus, and it is probable that as these other species are described in more detail, further distinguishing characters will be added.

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First Record of Whitebait Smelt (*Allosmerus elongatus*) from Juan de Fuca Strait, British Columbia

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BARRACLOUGH, W. E., AND R. M. WILSON. 1971. First record of whitebait smelt (*Allosmerus elongatus*) from Juan de Fuca Strait, British Columbia. J. Fish. Res. Bd. Canada 28: 1681.

The whitebait smelt *Allosmerus elongatus* (Ayres) is recorded from British Columbia for the first time on the basis of three specimens from Juan de Fuca Strait caught November 2, 1969.

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Le 2 novembre 1969, on a enregistré pour la première fois en Colombie britannique, dans les eaux du détroit de Juan de Fuca, trois espèces de l'éperlan blanchaille *Allosmerus elongatus* (Ayres).

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THREE specimens of the whitebait smelt, *Allosmerus elongatus* (Ayres), were caught in an otter trawl by D. Guyan, captain of the trawler *Bon Accord II*, while fishing about 2 miles west of San Juan Point in 70 m off the lower west coast of Vancouver Island in Juan de Fuca Strait on November 2, 1969.

Although this species ranges from San Francisco Bay and possibly San Pedro, California (Clark 1940), north into Juan de Fuca Strait, Washington, it has not been reported previously from the immediate coastline of British Columbia. It may have been caught by fishermen in the past but remained undetected by its overall similarity to other species of smelts in these waters that are more common and more abundant.

In California, Roedel (1948, 1953) reported that several members of the true smelts, Osmeridae, are called "whitebait" when they are small, but two species, the night smelt *Spirinchus starki* (Fisk) and *A. elongatus*, form the bulk of whitebait catch. The fishery in California is of minor commercial significance, with landings chiefly at Eureka and the catch sold entirely on the fresh-fish market.

McAllister (1963) has examined specimens from San Francisco Bay and provides a synonymy, a complete diagnosis, and description of the genus and species. In his examination of these specimens from British Columbia, he noted the absence of pyloric caeca (personal communication), which is the diagnostic feature separating this species from all other Osmeridae in these waters. It is further distinguished by the single large elevated canine on the middle of the vomer plus an occasional smaller recumbent lateral on either side; the long predorsum; and the long, pointed snout and large orbit diameter, both of which exceed $\frac{4}{5}$ of the caudal peduncle depth. The specimens have been deposited in the National Museum of Natural Sciences, Ottawa, Ont. (catalogue number NMC70-53). The species reaches a length of 229 mm (Roedel 1953).

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This issue of the Journal of the Fisheries Research Board of Canada is dedicated to Dr Cyril Berkeley and to the memory of the late Mrs Edith Berkeley.

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